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INSECTS OF HAWAII

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INSECTS OF HAWAII

A Manual of the Insects of the Hawaiian Islands, including an Enumeration of the Species and Notes on their Origin, Distribution, Hosts, Parasites, etc.

by **ELWOOD C. ZIMMERMAN**

Associate Entomologist, Experiment Station,
Hawaiian Sugar Planters' Association; Curator
of Entomology, Bernice P. Bishop Museum

VOLUME I -

INTRODUCTION

Sponsored by

BERNICE P. BISHOP MUSEUM • EXPERIMENT
STATION, HAWAIIAN SUGAR PLANTERS'
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1948

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To My Friends and Counselors

CHARLES MONTAGUE COOKE, JR.
OTTO HERMAN SWEZEY

Keen Observers

Learned, Unselfish Servants of Science

By Whose Gleanings from Nature Men Will Prosper

FOREWORD

Need has long existed for an up-to-date and comprehensive work on the insects of the Hawaiian Islands—a work which would be of immeasurable benefit as a handbook for scientists, as a textbook for students, and as a reference for horticulturists, quarantine officers, and specialists in our sugar and pineapple industries and other branches of Hawaiian agriculture. Indeed, as agriculture of a highly specialized and scientific order is our basic economy, it is hard to visualize anyone in Hawaii who would not benefit, directly or indirectly, by the existence of a detailed monograph on the insects which each year cause damage amounting to hundreds of thousands of dollars.

Many insects of Hawaii are common to other Pacific islands and to many continental areas as well. A basic book on the insects of the Hawaiian Islands will serve as a solid foundation for studies of the insects of islands elsewhere in the Pacific Basin, and should in itself prove interesting and useful to investigators the world over.

Since 1934, when he returned from an expedition to the south Pacific, Elwood C. Zimmerman has been working on just such a study. He embarked upon his ambitious project as a young man who (perhaps fortunately for those of us who will benefit by it) was not fully aware of the enormity of the task nor of the obstacles and diverse activities which were to impede its progress during the succeeding years. Even without the inevitable interruptions, the project could never have been completed on a forty-hour-a-week basis; and it was only by dint of determination and a devotion involving very considerable personal sacrifice that the basic work on an anticipated twelve- to fifteen-volume set was done and the first five volumes completed for publication.

Mr. Zimmerman is eminently well qualified for this courageous undertaking, the comprehensiveness of which is staggering in this day of specialization. These first five volumes justify the confidence placed in him over the span of fourteen years which he devoted to this work—work which was interrupted by exploratory trips to many Polynesian islands and by the publication of more than one hundred papers.

It had been originally intended that *Insects of Hawaii* would be published by the Bishop Museum. The text expanded to such proportions, however, as to impose an excessive financial burden on that institution, and prospects for publication became indefinite. The Experiment Station of the Hawaiian Sugar Planters' Association, whose staff Mr. Zimmerman had joined in 1946, recognizing the great practical need for this work, encouraged the author to continue his labors. Early in 1948, the manuscript, accompanied by a grant-in-aid from the Experiment Station to the amount of one-half the cost of publication of the first five volumes, was offered to the University of Hawaii Press. This sum was matched by the University of Hawaii and the manuscript was accepted by the University of Hawaii Press. Through this cooperative arrangement, the early publication of the first five volumes of *Insects of Hawaii* was assured.

The University of Hawaii is proud to join with the other institutions in the publication of *Insects of Hawaii*, and wishes Mr. Zimmerman all success in the completion of his valuable contribution to the store of scientific knowledge.

GREGG M. SINCLAIR

President, University of Hawaii

PREFACE TO THE FIRST FIVE VOLUMES

This work was started soon after the completion of the Bishop Museum's Mangarevan Expedition to southeastern Polynesia in 1934. I arrived in Hawaii following that unique field experience filled with the enthusiasm and spirit of scientific research, fresh from exploration in some of the very islands which thrilled Charles Darwin, and instilled with the marvels of evolution and biogeography so vividly displayed by island life. I found Hawaii to be the most remarkable of any group of islands I knew, and I soon felt a great need for a revisional work which would contain essential facts about the Hawaiian insect fauna, would serve as a guide to all students, and would give workers here and abroad a better appreciation and appraisal of our accomplishments and our problems. The monumental *Fauna Hawaiiensis* is available, but is far out of date in many respects and is inadequate in many ways for our present purposes; it is largely the repository of original descriptions. Consequently, I determined to assemble a working outline of the Hawaiian insects. These five volumes represent a part of my results.

Plan of the Work.—These first five volumes include the "Introduction" and, in phylogenetic order, cover the groups of insects from the Thysanura through the Homoptera. I had hoped to include all this material in a single book, but the text increased until it was decided to divide it into five volumes. Thus, the volumes may be purchased or used separately, and many specialists no doubt will want to obtain only the volumes covering their special fields of interest.

There remain to be treated in subsequent volumes the following orders: Ephemeroptera, Neuroptera, Trichoptera, Lepidoptera, Coleoptera, Strepsiptera, Hymenoptera, Diptera and Siphonaptera. I want to prepare also a volume on the history of Hawaiian entomology and to issue a general checklist of the recorded species of all the orders. Most of the fact-gathering and bibliographic work for these future volumes is complete. Final preparation and publication rest largely upon time and facilities being made available for the work.

This work has been written to be used in conjunction with the *Fauna Hawaiiensis* and the *Proceedings of the Hawaiian Entomological Society*. It is assumed, therefore, that serious users will have these fundamental sources of Hawaiian entomology available and will use them as adjuncts to these pages. One or more of the leading textbooks of general entomology and a glossary should also be at hand.

The total number of insects listed in these first five volumes is about 1,100. The *Fauna Hawaiiensis* included about 500 in the same groups. Hence, these volumes show an increase of about 120 percent in the number of species known to occur in Hawaii. The proportion of native to immigrant species as listed herein is about 672 native species to 420 adventive species. There is a large number of endemic species yet to be described, and several recently immigrant species are

not recorded here. The total number of known Hawaiian insects is approaching the 6,000 mark.

An attempt has been made to present in these volumes an enormous assemblage of information in compact form. Much time has been devoted to the preparation of keys (about 275 of them in the four systematic volumes) in the belief that they will, when used with the illustrations, take the place of individual descriptions. References are given to all original descriptions and to other pertinent literature, and these will have to be referred to when necessary.

There has been assembled a surprisingly large literature about Hawaiian insects. However, the more important bibliographies of particular groups of species usually are not very extensive. Thus, one learns quickly that R. L. Usinger's major work on the Hawaiian *Nysius* bugs was published by the Bishop Museum in 1942, and when the contracted reference "Usinger, 1942:60" is given, one will soon know what to look for without referring to the detailed bibliography for the complete title. I realize that this system has certain disadvantages, but I believe that its merits overshadow its faults.

Most abbreviations, including authors' names, belong in working notes. They have been kept to a minimum in this text, because I consider them confusing, particularly to foreign scholars and students, and not infrequently to the most skilled specialists.

No attempt has been made to compile complete data on the extra-Hawaiian distribution of all of the non-endemic insects, but the information which has come to hand has been incorporated. Many of the adventive species are found on more of the Hawaiian Islands than are recorded for them, but unless records have been seen in literature or specimens examined, I have been unable to complete the distribution lists. Specialized collecting will supply information to close many gaps, and it is expected that some readers will take pleasure in trying to supply new distributional data and annotating their copies of the text. The publishing of incomplete records should be a stimulant to such activity. Complete listings of synonymies have not been included under the adventive species, but those which have appeared in Hawaiian literature have been listed. Also, I have not included all of the misidentifications, the immigrant and introduced species which apparently have failed to become established here, or those which have been recorded by genus only, or those which belong to the quarantine records.

Inevitably, parts of this text are already out of date; the new discoveries and reports of the active group of Hawaiian entomologists will make it further behind the times as it goes through the time-consuming intricacies of publication. I plan, tentatively, to publish each year a supplemental paper in the *Proceedings of the Hawaiian Entomological Society* in which notes, corrections and certain additions will be incorporated—or perhaps someone else will undertake the task or carry on after me. Thus, one can keep his volumes annotated and corrected by referring to the *Proceedings*. This manuscript was closed with the year 1946, and only a few of the species which have come to attention since that year have been added.

Reference should be made to the *Proceedings of the Hawaiian Entomological Society* for pertinent information after the 1946 issue of that journal.

Before I began writing this text, I had not worked on any of the groups contained in these first volumes. They and their literature were generally unfamiliar to me. Obviously, this has been a serious handicap, for one of the greatest difficulties encountered when writing about unfamiliar groups is the proper evaluation to assign to various features. This deficiency will be, I fear, only too evident to my critics.

I have read the manuscript and proofs for this work many times, but there has not been a reading when I did not have some new material to add, or that I wanted to add, which had come to hand since the last reading. A few hours spent in the garden or on a field trip usually reveals some or many new things which I should write more about. There is no end!

This work has its share of errors—errors of omission and commission. What appear to be facts today may prove to be errors tomorrow; it is inevitably thus in science. Of course, there are also those many slips of the pen and the typographical errors that will escape notice until the printed page is done. My readers are encouraged to find, reveal and correct the errors, and the keenness of their criticism will be a measure of their interest in this work. This text can be made better only by use, revision and correction. Some sections of it are presented here more as working outlines than as completed projects; it will take years of study to perfect them. I urge my readers to send corrections and criticisms to me or to the Secretary of the Hawaiian Entomological Society so that they may be made available to all interested persons.

It is obvious that one of the major contributions of this work is its several thousand illustrations. These are of paramount importance in conveying clear opinions without excess verbiage. They speak for themselves. There are not enough illustrations here, and many of them are not as good as they should be. I hardly need to say that it is difficult and expensive to illustrate such a manual. One often has only imperfect specimens to work with (and, surprisingly enough, this applies to the common species as well as to the rare ones); or they do not lend themselves to good rendering in this technique or that; or there may be no specimens available to illustrate. I have been fortunate, however, in having the aid of some highly skilled artists who are responsible for the splendid reproductions offered here. (They are not to be blamed for the unsigned sketches made by the author, however.) I have encouraged them to render their skills in various ways, so that we could present a variety of types of entomological art work. It is regrettable that only a modest fund was available for the furnishings of drawings; hence, some of the sections are not illustrated as adequately as they should be. Here, again, we have compromised, but the artists have given us a set of illustrations of great and lasting value which would enhance the value of any text.

Acknowledgments.—To acknowledge the generous cooperation I have received is a pleasure. This work has been accomplished through the cooperation of many

men and women in several institutions at home and abroad. Without their aid, *Insects of Hawaii* could not have been written.

First of all, I wish to thank the Director of the Bishop Museum, Peter H. Buck, and the Trustees of the Museum. Under their direction I have been given ample quarters and allowed to carry on this task as a principal project of the department of entomology. I particularly want to thank them for having trust in me as a scientist, for assigning me a quiet office, with appurtenances, where I could work, plan and think with a minimum amount of disturbance and outside interference while doing the job. Few men have had such an opportunity; perhaps this is one reason why such monographs are not common. To write such a long and complicated report, one must have a quiet retreat and be left undisturbed as much as is necessary to accomplish the task. Even under the best of conditions, such a work is extremely difficult and trying on one's physical resources. Interference, interruptions and lack of quiet make for errors and inefficiency. I wish to thank them also for grants-in-aid which enabled me to have many of the beautiful drawings made by leading entomological draftsmen, for many kind favors and for their interest in and patience with a long-term project.

The Experiment Station, Hawaiian Sugar Planters' Association, where I have been employed since the beginning of 1946, under the very able direction of Harold L. Lyon until March, 1948, and now in the capable hands of L. D. Bayer, has assigned me the task of completing *Insects of Hawaii* as my major project. Although Dr. Bayer has assumed the directorship since these first five volumes were completed, he has shown keen interest in the project and has been kind and generous in his support of my work. Dr. Lyon has shown a singular interest in the monograph and has made me feel that I was doing something worth while. He has been cheerful and generous with his aid, and I have been buoyed up by his continued encouragement. He has always given freely of sound advice and has championed the cause over the roughest of ways.

The Trustees of the Hawaiian Sugar Planters' Association have given the project excellent support. They are to be thanked especially for their broad-minded approach to the problems of basic research in an industrial institution. They are keenly aware that some projects which appear to be far within the realm of "pure" research frequently are ones which pay large dividends of lasting value. I hope that these fruits of my labors will repay the Hawaiian sugar industry for its large investment in these pages. There are few industries which can boast of such support to basic science, but this is a tradition of long standing with the H.S.P.A.

The Board of Regents of the University of Hawaii have contributed generously to the publication fund and have made it possible for the work to be issued by the University of Hawaii Press. The University's President, Gregg M. Sinclair, has given the enterprise his full support and has lent an encouraging and helpful hand.

There are two men to whom I owe more than I can express adequately on these pages. In the light of the knowledge of the natural history of Hawaii held

by these learned, but all too modest, naturalists, my own learning appears meager and immature. I have written down much of what I know, but they have more information about the Hawaiian flora and fauna stored in their minds than I shall ever know. I refer to C. Montague Cooke, Jr., and Otto H. Swezey. They have been my close friends and advisors and my valued companions on expeditions to the south Pacific. They have been storehouses of knowledge from which I have drawn heavily. Such men are made rarely.

Dr. Cooke has been as a leading and guiding light to me for many years, and whatever success I may have achieved or shall achieve in my studies of the Pacific is in large measure because of him. I consider myself his very willing and fortunate protégé. He has been more than a friend and colleague—he has been as a father to me. I can never honor him enough.

Dr. Swezey has been a close companion ever since I came to Hawaii. He has guided me and introduced me to the intricacies of the Hawaiian insect fauna. He has aided me in ways too numerous to mention. His knowledge of the insects of our islands has been rivaled only by that of Dr. Perkins. For nearly half a century he has been responsible for more of the basic records in our entomological literature than any other person. I may try to follow in his footsteps, but I can hardly hope to catch up to him. I shall always be awed by the scope of his knowledge of Hawaiian natural history.

The entomological staff of the Experiment Station, H.S.P.A., took an active interest in this text many years before I was asked to join that institution, and the successful completion of this work is due in large measure to the interest and active participation of the Experiment Station. A large number of the photographs were made gratis by the Experiment Station before I was employed there, and the library, collections and other facilities were generously placed at my disposal. To C. F. Pemberton, Entomologist, in charge of the Department of Entomology, I am especially indebted. His interest, guidance, aid and encouragement have helped me carry on in the face of many difficulties. To him belongs much of the credit for seeing that these volumes finally have been published. F. X. Williams has been an ever-flowing spring of freely given knowledge. R. H. Van Zwaluenburg read the systematic text in manuscript before I joined the Experiment Station, and his aid has been continuous and invaluable since I began the work. Unfortunately, I have had no personal contact with R. C. L. Perkins, distinguished retired member of our staff, but we have carried on through correspondence, and he has given me much help. Further acknowledgments to our staff appear in appropriate places in the text.

The artists whose illustrations appear in this work have made an outstanding contribution in supplementing the text. Nearly all the photographs were made at the Experiment Station by W. Twigg-Smith and J. T. Yamamoto, mostly by Mr. Yamamoto. Frieda Abernathy, now of the Division of Entomology and Parasitology, University of California, has produced a large set of beautiful ink and wash drawings which are a splendid contribution in themselves. R. L.

Uisinger supervised her drawings of the Heteroptera, E. O. Essig those of the aphids and S. F. Bailey those of the Thysanoptera. We were fortunate in having Arthur Smith make a fine set of drawings, mostly of type specimens, at the British Museum (Natural History), where his work was supervised by N. D. Riley and W. E. China. G. F. Ferris took such an interest in the text that he supplied an unequaled array of plates of coccids. Professor Ferris's contribution calls for special comment in volume 5. F. X. Williams made a number of drawings especially for this work and supplied a large number of his original drawings used in previous publications and rearranged here. I am deeply indebted to all these artists who have given much to aid workers both in Hawaii and abroad.

It is a pleasure to acknowledge the aid given by several librarians who have done much to help with the difficult tasks involved in bibliographic work. Mathilde M. Carpenter, U. S. National Museum, and Mrs. M. A. Frazier, Museum of Comparative Zoology, Harvard, gave freely of their time during my research visits in 1941. The library facilities at the University of California and the California Academy of Sciences were used extensively during my visits to those centers. I am indebted to the Bishop Museum for making it possible for me to visit these institutions in 1941 to consult literature not available in Honolulu. In Hawaii, Mabel Fraser, Experiment Station, H.S.P.A., and Margaret Titcomb, Bishop Museum, have contributed much to this work. For more than a dozen years Miss Fraser has borne cheerfully the brunt of many of the most difficult of the bibliographic problems encountered. During the past few years her assistant, Jean Dabagh, has helped in many ways.

Harold St. John, University of Hawaii, and Marie Neal, Bishop Museum, have helped with the identification of hostplants for many years, and I am grateful for their aid.

To C. F. W. Muesebeck and his competent staff of the Division of Insect Identification, U. S. Bureau of Entomology and Plant Quarantine at Washington, I am deeply indebted for favors too numerous to mention in detail here. Although he and his staff are continuously overwhelmed by work, not one of my many requests for aid has been ignored. They were particularly helpful during my visit to Washington in 1941, and they were joined by E. A. Chapin and R. E. Blackwelder of the National Museum, who also did much to make my research successful. Additional acknowledgments will be found in succeeding volumes.

Likewise, N. D. Riley and his associates at the British Museum (Natural History) have contributed much to the molding of this series of volumes.

My close friend and colleague since school days, R. I. Uisinger, has taken an active interest in *Insects of Hawaii* and has given whole-hearted aid and encouragement.

There remains to be thanked a group of people who all too frequently remain as anonymous contributors to published works. I am deeply grateful to Juliette Wentworth, editor, University of Hawaii, who has shown unusual understanding in the preparation of this technical manuscript for the printer. It has been a rare pleasure to work with her, and her broad-minded approach to editorial complexities

and her understanding of the author's problems has been most gratifying. She has done much to make these volumes better for the users. She has had the able association of Margaret Blegen, and Jean Kangeter, Helen Matthews and Richard S. Cowan have given aid in the reading of proof. Typing of most of the manuscript was done by Mrs. S. Austin, Patience Wigger Bacon and Violet Sumi at the Bishop Museum. Thomas Nickerson, head of the Office of Publications, University of Hawaii, has taken a keen interest in the work and is largely responsible for the facility with which it has been issued from the University Press, and I am deeply indebted to him for many kind favors. Leonard Tuthill, Editor of *Pacific Science* and Associate Professor of Entomology at the University, has been an active participant in the editorial and publication details. The printing and engraving departments of the Honolulu Star-Bulletin have given excellent cooperation, and these printed pages and the illustrations they bear speak for them and the care they have taken in setting the type and making the engravings.

E.C.Z.

Honolulu, Hawaii
June, 1948

INTRODUCTION TO VOLUME 1

The text of this volume of *Insects of Hawaii* was read, in abstract form, as the address of the retiring president of the Hawaiian Entomological Society, December 14, 1942. It is premature, for it would have been better to have written the discourse after this proposed series of volumes had been completed and after many intricate problems had been investigated more thoroughly. But the completion of such a task as this involves many years of study, and who knows whether conditions will enable the author to finish his work? However, this presentation is justified as stimulation to further study, as a foundation upon which to build and as a review of pertinent problems.

The foundations for this essay were laid during the Bishop Museum's Mangarevan Expedition to southeastern Polynesia in 1934, and from then until the outbreak of the recent war most of the remaining data were assembled. It was not thought that so many years would pass between the presentation of the manuscript in 1942 and its publication. Much has been accomplished in the Pacific since this paper was read. Thousands of new soundings have been made, the "guyots" of Hess ("sea mounts" of some observers) have been described, deep holes have been drilled on Bikini, thousands of specimens and a large amount of new information have been assembled and some notable papers have been published. The pressure of other work made it impossible for me to revise the entire manuscript to include many of the new facts, but I have not seen any reports which would change the conclusions put forth here. This thesis remains, then, essentially as it was presented to the Hawaiian Entomological Society in 1942.

I fear that my "insular isolation" in some ways has had a delimiting effect upon my work, and perhaps many of the errors and weak points in this volume could have been avoided had I been exposed to the "rigorous competition" of a "continental environment" during the preparation of the final draft. One's work is bettered by association with students keenly interested and actively engaged in the same and bordering fields of endeavor, but many authorities have not been available for personal consultation, nor has it been possible for them to have seen the manuscript. However, I have been fortunate especially in having close and stimulating association with several leading students of Polynesia who are resident in Hawaii. C. M. Cooke, Jr., has been particularly interested in the text for this

introductory volume and has been a source of constant aid, enlightenment and encouragement. Dr. Cooke read much of the manuscript, and his constructive criticism has been most helpful. He and his assistant, Yoshio Kondo, have given me much help with problems concerning Polynesian land molluscs. O. H. Swezey has aided in many ways with several sections. C. K. Wentworth and W. O. Clark read the section on geology, H. E. Gregory gave aid on various problems, and F. X. Williams read the chapters on dispersal and development. Harold St. John and F. R. Fosberg have given valued aid on Polynesian botany. Ernst Mayr and Dean Amadon of the American Museum of Natural History have given much help during our discussions of problems of Polynesian birds. Dr. Mayr has been a constant source of encouragement, and his well-known publications have been a source of inspiration. R. H. Van Zwaluwenburg has read all the proof sheets, and I am much indebted to him for his aid and interest in the work. I owe these men many thanks.

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INSECTS OF HAWAII

CHAPTER 1

GEOLOGICAL HISTORY OF HAWAII

Time is a sort of river of passing events, and strong is its current; no sooner is a thing brought to sight than it is swept by and another takes its place, and this too will be swept away.

—*Marcus Aurelius*

Although the gross features of the geology of the Hawaiian Archipelago are comparatively simple, I might wisely hesitate to enter into a discussion of a field so far outside my own. However, there are those who still persist in looking for the mystical in the islands of Oceania and who insist upon vast and ancient Pacific continents or great land bridges that are supposed to have vanished beneath the waves to account for the development and distribution of the particular groups of organisms composing their special fields of research. At the risk of repetition for those few workers who have studied the geology of some Polynesian islands, a discussion review of the geological foundations of Hawaii is essential for the proper understanding of the subjects that follow. Moreover, even the rudiments of the established geological facts regarding these islands are not wholly familiar to the majority of biologists.

As a result of geological study, it is known that the Pacific Basin is underlain by heavy basaltic rock; that in the continents generally lighter or metamorphosed rocks rest on heavier under-layers; and that continental shelves extend for various distances under shallow coastal waters and then terminate rather abruptly at the edge of the deep water which is of remarkably uniform depth of about 12,000 to 15,000 feet and more in the true Pacific Basin; that the volcanoes now above sea level have risen from great depths and have been built of basic rock, and that in no islands in the central Pacific Basin have true continental rocks been found. So far as it is known to geologists, the only pre-existing extensive land masses in the tropical Pacific, since the rise of modern floras and faunas, are those west and north of Australia and on the New Guinea-New Caledonia-New Zealand axis, possibly extending eastward to near the Tongan Trough in the neighborhood of Fiji. There is no geological evidence to indicate the existence of any large land masses east of Tonga and Fiji.

However, in spite of the carefully recorded geological data, some biologists continue to raise great masses of millions of square miles of sea bottom 12,000–18,000 or more feet, and then sink them into oblivion without a trace of the requisite diastrophic action, to account for the distribution of a few organisms whose presence on certain islands constitutes a puzzling problem to the worker in question. Thus, Jeannel (1937), to account for the presence of two tiny ground beetles in Hawaii, believes that the islands once formed a part of a great land

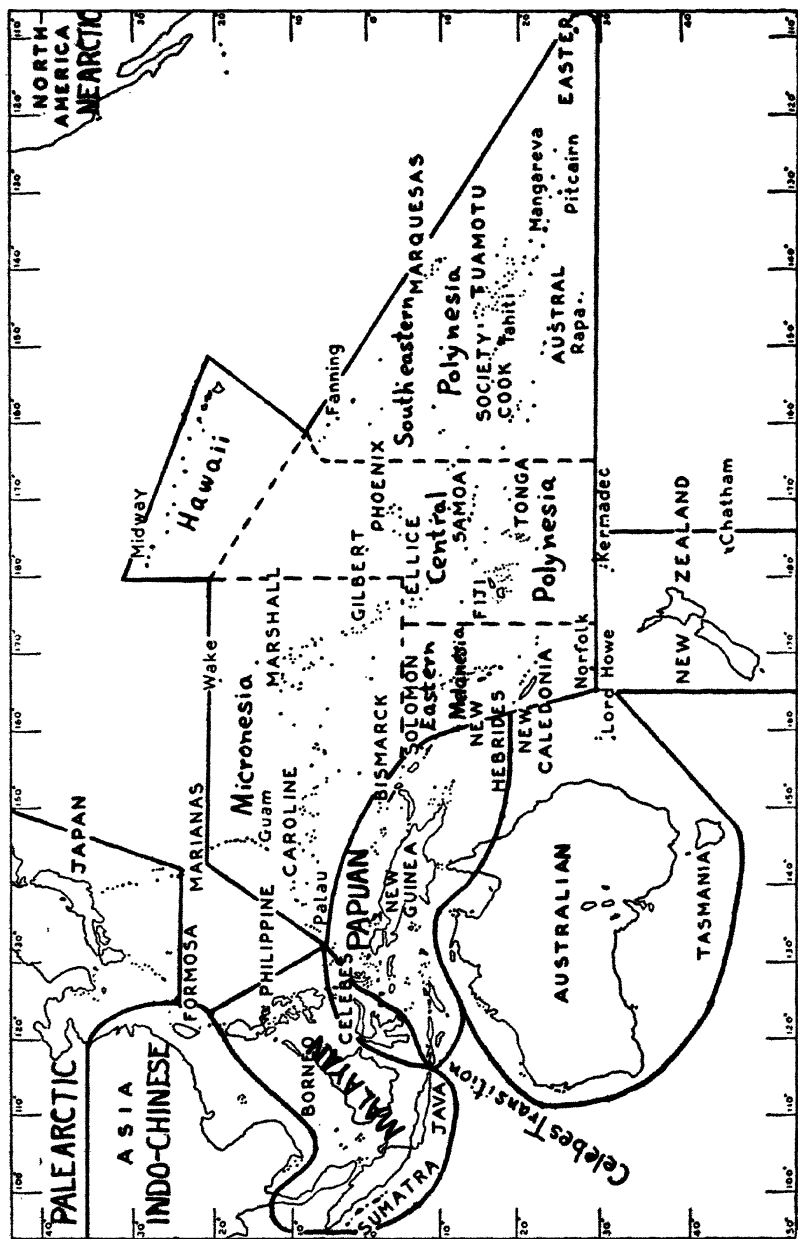


Figure 1.—Map of the central and western Pacific showing zoogeographical divisions. The five provinces of Polynesia are connected by broken lines and labeled in lower-case letters.

mass connected to "Gondwana" and that the beetles migrated to Hawaii in Jurassic times. The fact of the matter is that these two beetles were recently accidentally introduced with plants imported into Hawaii and are now established in the soil at the Sugar Planters' Experiment Station in Honolulu! Crampton (1932, and recent discussions) would "create" a great land mass extending from the Marianas and Palau Islands over 5,000 miles to southeastern Polynesia to account for the distribution of a single genus of land snails and gives no heed to many other land snails of the same area whose distributions are quite the opposite of his proposed land mass, to say nothing of other genera of plants and animals. It is difficult to conceive that such a great continental area would founder and leave only the few organisms now used for support by the "continentalists" as evidence of its existence. All our continents have developed great and distinctive floras and faunas, and the partial submergence of any of them would leave on isolated areas abundant evidence of the characteristic biota, not just a few snails.

As said elsewhere (Zimmerman, 1942:282):

So many continents and land bridges have been built in and across the Pacific by biologists that, were they all plotted on a map, there would be little space left for water. Whenever a particularly puzzling problem arises, the simplest thing seems to be to build a continent or a bridge, rather than to admit defeat at the hands of nature, or to consider the data at hand inadequate for solving the problem. Most of the land bridges suggested to account for the distribution of certain plants and animals in the Pacific create more problems than they solve. If the central and eastern Pacific ever included large land areas and bridges, there would be some indication of the consequent peculiar development of the fauna and flora, but there is no such evidence.

WHAT IS HAWAII?

Hawaii is a great chain of 18 islands, several satellite islands and various islets, reefs and shoals extending on a northwest-southeast line from about $178^{\circ} 29'$ to about $154^{\circ} 51'$ west longitude between about $18^{\circ} 5'$ and $28^{\circ} 25'$ north latitude, an extreme length of over 1,500 nautical miles (1,660 nautical miles has been given as the extent from Hawaii to an unnamed shoal 280 miles from Kure) and a maximum spread of a little more than 600 miles in latitude. The northwestern island is a coral atoll; the southeastern island's volcanic summit rises to the maximum Hawaiian elevation of 13,784 feet. The islands are "north sea" islands, for the southernmost island is about 1,100 miles north of the equator. This line of islands may be divided into two groups. Those islands extending southeast from Niihau and Kauai to Hawaii are spoken of as the main or windward group; the remainder to the northwest, called the leeward group, consists of small reefs, islets or rocks which support only a small number of indigenes. In this paper, then, the entire chain of islands will be considered, and the two groups will be referred to as the main, or high, islands and the leeward islands. The main group consists of eight islands and several satellite islets. However, two of these islands, Niihau and Kahoolawe, were so completely denuded by grazing animals and their native products brought so close to extermination so many years before

natural history surveys were begun in Hawaii that they are mostly omitted from the discussion because we have almost no knowledge of their native floras and faunas. Therefore, the biota of the six main islands of Kauai, Oahu, Molokai, Lanai, Maui and Hawaii forms the foundation of our work.

The northernmost island of the leeward group is about as far north as the mouth of the Mississippi River, or about 200 miles south of Shanghai; the southernmost island is as far south as Mexico City, or approximately at the same latitude as the most northern tip of the Philippine island of Luzon. The north and south spread of the main islands in latitude is about equivalent to that of Cuba, and the length of the group of main islands is somewhat more than one-half the length of the island of Cuba. The length of the entire chain is about equal to the distance between Montreal, Canada, and Havana, Cuba, or between London and Moscow. The length of the main group of islands approximates the distance between Boston and Washington, D. C., or from Dover to Belfast.

The islands lie in the mid-Pacific. The nearest continental land is the coast of California to the east, or the Aleutian Islands to the north; both of these areas are about the same distance from the main islands. San Francisco is 2,091 nautical miles from Honolulu. Dutch Harbor, Unalaska, is somewhat closer. The nearest high islands (volcanic, that is) to the main islands are the Marquesas, the nearest of which is approximately 2,000 miles from the southern tip of the island of Hawaii. If we use Honolulu as a reference-point, the following distances are significant:

Yokohama, Japan	3,394 miles
Hongkong, China	4,857 miles
Manila, Philippines	4,767 miles
Sydney, Australia	4,420 miles
Auckland, New Zealand	3,840 miles
Suva, Viti Levu, Fiji	2,783 miles
Pago Pago, Tutuila, Samoa	2,276 miles
Papeete, Tahiti, Society Islands	2,381 miles
Panama Canal	4,685 miles

The nearest island to any of the Hawaiian islands is the coral atoll of Johnston Island, which is about 600 miles from the nearest main island, Niuhau, and about 450 miles from the nearest leeward island, French Frigate Shoal. Directly to the south of the main islands, a string of atolls, known as the Line Islands, connects with the Society Islands and the Tuamotu Archipelago. This line of coralline islands begins at Kingman Reef, which is about 850 miles south of the island of Hawaii, and continues southward through Palmyra, Washington, Fanning, Christmas, etc. The nearest islands to the southwest, beyond Johnston, are the coralline Gilbert and Marshall Archipelagos, which average about 2,000 miles from Honolulu (some of the Marshalls are 1,200-1,500 miles from the most leeward Hawaiian islands), and the Phoenix Islands, the nearest of which are 1,600-1,700 miles from the nearest main island; Howland and Baker are about 1,500 miles from French Frigate Shoal, the nearest Hawaiian island. To the west lies the isolated coral atoll of Wake, about 2,000 miles from Honolulu, or about 1,100 miles from the nearest leeward island (Kure). Then come the Marianas,

which are all over 3,000 miles from the nearest main Hawaiian island and over 2,000 miles from the most westward of the leeward islands. There is no land to the north of Hawaii until the Alaskan Peninsula and the Aleutian Islands are reached. The nearest of the Aleutian Islands are about 1,400 miles from the most northern Hawaiian island, Kure, and nearly 2,000 miles from the nearest main island; and there is no deep-sea island between Hawaii and the North American continental shelf.

AREA, ELEVATION, ETC.

The present areas of the small leeward reefs, rocks and islets are negligible, for they total only a few square miles, and for comparative purposes may be omitted from this discussion. The accompanying table has been compiled from data assembled by Wentworth (1939).

Only two of the United States, California and Washington, have greater ranges in elevation. Only California, Washington and Colorado have mountain peaks more than one foot higher than Hawaii's 13,784-foot Mauna Kea.

The total area of 6,435 square miles may be compared with some other areas with advantage to the discussion farther along in this paper. This area is equivalent to about 1/1,243 part of North America, 1/470 of continental United States, 1/457 of Australia, 1/24 of the state of California, 1/16 of the combined North and South Islands of New Zealand, 1/5 of Ireland, or 4/5 of the state of Massachusetts. The following areas of other islands, in approximate areas in square miles, may be compared:

New Guinea	312,329	Solomon Islands	16,975
Borneo	285,000	Formosa	13,892
Sumatra	164,480	New Caledonia	8,500
Philippine Islands	114,400	Fiji Islands	7,070
Luzon 40,814; Mindanao 36,906		New Hebrides Islands	5,700
Celebes Islands	69,255	Samoa Islands	1,200
Java	50,000	Society Islands	600
South Island, New Zealand	58,525	Marquesas Islands	400
North Island, New Zealand	44,468	Tonga Islands	385

HAWAII: OCEANIC OR CONTINENTAL?

This problem involves the evaluation of both geological and biological criteria. In the following commentary, some of the salient facts regarding the building of the islands from the ocean floor, and the life supported by them, will be discussed.

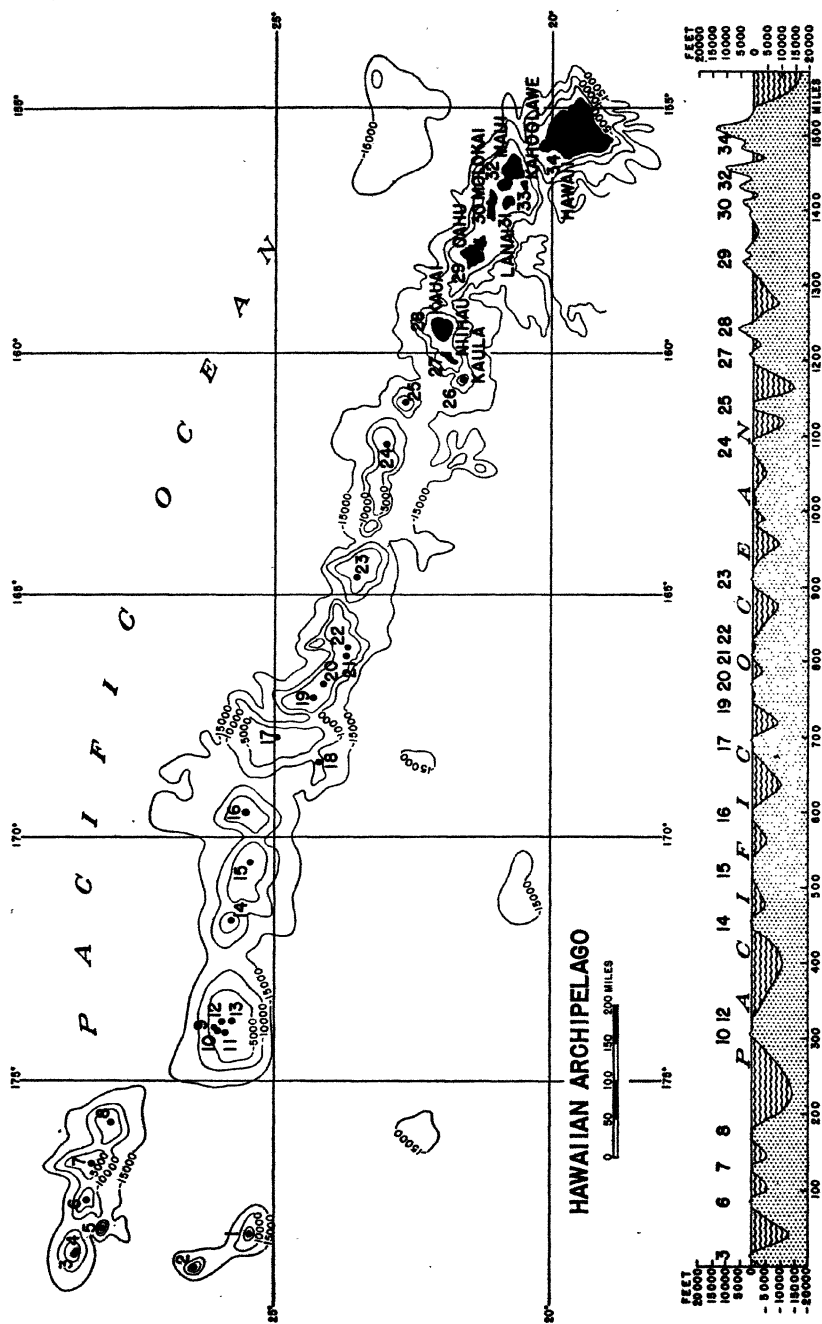
The Hawaiian Islands are oceanic; there is no evidence whatsoever to support the contention that they are of continental origin or character, or that they were ever joined together in an elongate subcontinental land mass or even in a continuous subaerial mountain range. The great body of evidence amassed from the study of both geology and the biota supports the oceanic opinion: "... the eastern oceanic insect faunas could not have become what they are with any great land areas or bridges in the central Pacific; their very character precludes those possibilities. The known groups are the results of overseas sifting; there are too many groups lacking for any other means of dispersal to have been involved." (Zimmerman, 1942:282.)

SIZE AND LAND AREA OF MAIN ISLANDS OF THE HAWAIIAN ARCHIPELAGO

ISLAND	EXTREME LENGTH	EXTREME BREADTH	PERIMETER	EXTREME ELEVATION	AREA = (TOTAL = 6,433)	AREA OVER 20 MILES INLAND	AREA 10-20 MILES INLAND	AREA 5-10 MILES INLAND	AREA 0-5 MILES INLAND	GREATEST DISTANCE FROM COAST
	miles	miles	miles	feet	sq. miles	sq. miles	sq. miles	sq. miles	sq. miles	miles
Hawaii	93	76	319	13,784	4,030	346	1,365	1,110	1,209	28.5
Maui	48	26	160	10,025	728		2	172	554	10.6
Oahu	44	30	190	4,025	604		1	126	477	10.6
Kauai	33	25	112	5,170	555		6	177	372	10.8
Molokai	38	10	104	4,970	260				260	3.9
Lanai	18	13	53	3,370	141				141	5.2
Niihau	18	6	47	1,281	72				72	2.4
Kahoolawe	11	6	37	1,415	45				45	2.4

The breadths of the channels between the islands are roughly as follows in land miles:

Niihau-Kauai	17	Molokai-Lanai	9
Kauai-Oahu	73	Maui-Lanai	9
Oahu-Molokai	26	Maui-Kahoolawe	6
Molokai-Maui	9	Maui-Hawaii	29



THE PACIFIC BASIN AND THE DEPTHS OF THE SEA
IN THE HAWAIIAN AREA

The Pacific is the oldest, largest, broadest and deepest of the oceans; it has many characteristic features of its own; but it is the least known of the oceans. In spite of the lack of detailed surveys of many of the ramifying fields of oceanography, there are known some pertinent and dominant data regarding the gross features of the Pacific Basin which are fundamental to any research on the distribution and development of the biota. These criteria are all too frequently overlooked or are neglected by biologists. But they are basic—they cannot be ignored. Any theory concerning the distribution of plants and animals which fails to take these data into its primary scope has its foundations built upon unsound blocks—its very beginnings spring from error. Certain workers in the past have been prone to substitute daydreaming and wishful thinking for the less exciting, more laborious tedium of routine research when attempting to solve their individual problems of biogeography. Also, more often than not, some workers develop a theory to account for their particular problem and fail to take into consideration the all-important implications of such a theory on the study of the entire biota and on the sum total of the geology of the region included.

In describing the Pacific Ocean, I can do no better than to quote the summary of topographic relations written by H. E. Gregory (1928) after a number of years of intimate association with all phases of the study of the Pacific as Director of the Bishop Museum. Gregory says:

The Pacific Ocean is a huge affair: it is long and wide and deep. From Bering Sea to Wilkes Land on the Antarctic Circle the distance is 9,300 miles, and along the equator the distance is 10,000 miles—two-fifths of the circumference of the earth—and more than three times the width of the Atlantic. These great stretches of water form the axis of an area comprising more than 55,000,000 square miles—the area of the United States is about 3,000,000 square miles. The Pacific is nearly twice the size of the Atlantic and greater in area than all the continents and islands combined. The volume of Pacific water is incomprehensibly great. If all the lands above sea-level—plains, plateaus, and mountain systems—were piled into the Pacific they would sink to the bottom and be submerged at a depth of about 12,000 feet. If the water were drained from the Pacific the descent from the present shore line to the floor of the deepest valley would be greater than the present ascent to the loftiest Himalayan peak.

In a geological sense this vast water-filled basin comprises two parts: (1) The Pacific continental border and associated continental islands; (2) oceanic islands which have no genetic relation to continental masses. The line separating these two parts extends from New Zealand past the Kermadecs, Tonga, and Samoa, and continues northward in an undetermined position. West of this line the islands, shoals, and intervening spaces have been structurally parts of

Figure 3.—Map and profile of the Hawaiian Archipelago showing the submarine contours in feet. 1, unnamed shoal; 2, Bensaleux Reef; 3, Kure or Ocean; 4, Green; 5, Nero Bank; 6, Midway; 7, Gambia Shoal; 8, Pearl and Hermes Reef; 9, Lisianski; 10, Fisher Reef; 11, Minor Reef; 12, Neva Shoal; 13, Springbank Reef; 14, Laysan; 15, Maro (Dowsett) Reef; 16, Raita Bank; 17, Gardner Pinnacles; 18, Two Brothers Reef; 19, St. Rogatien Bank; 20, Brooks Banks; 21, La Pérouse Pinnacle; 22, French Frigate Shoal; 23, Necker; 24, Nihoa; 25, unnamed shoal; 26, Kaula; 27, Niihau; 28, Kauai; 29, Oahu; 30, Molokai; 31, Lanai; 32, Maui; 33, Kahoolawe; 34, Hawaii. (After Stearns, 1946. Cut loaned by U. S. Geological Survey, Honolulu.)

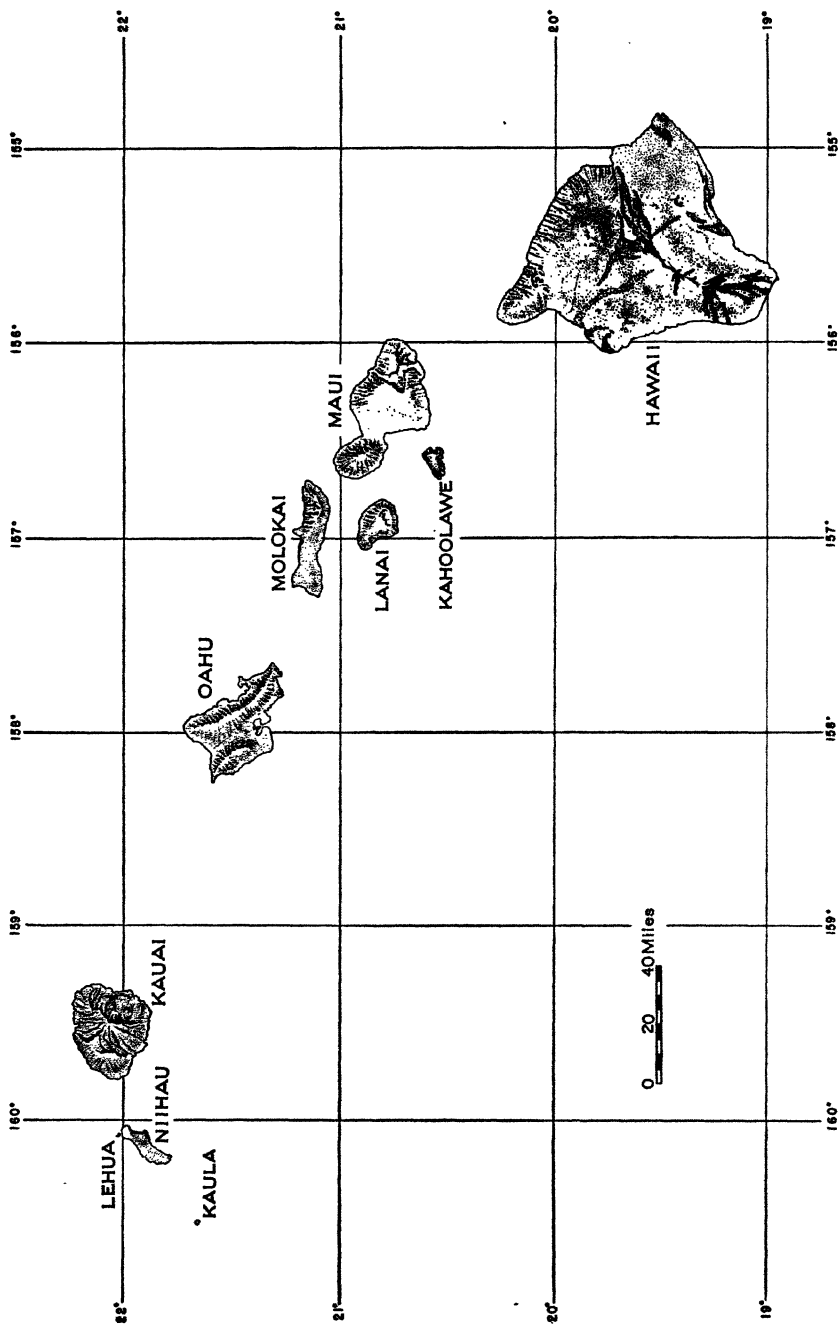


Figure 4.—The main islands of Hawaii. (After Stearns, 1946.)

large land masses. They have been submerged and emerged, connected and disconnected, in various combinations at several periods during geologic time. They occupy a region of general crustal unrest.

East of this changing border of an Australian-Asiatic continent and extending nearly to the American shores is the true Pacific depression, a submerged region of plateaus and intervening broad valleys from which rise mountain masses with relatively small areal bases. The general arrangement is a floor at profound depth from which rise volcanic masses as individual mounds or combined to form ridges or long, narrow submarine highlands. Most of these peaks and ridges terminate below sea-level and are revealed only by soundings; some of them terminate above sea-level and stand as islands. But they are true oceanic islands; they have never been parts of the continents of Asia, Australia, and America. They are all volcanic masses with outer slopes descending steeply to great depths. Some of them retain their original form;

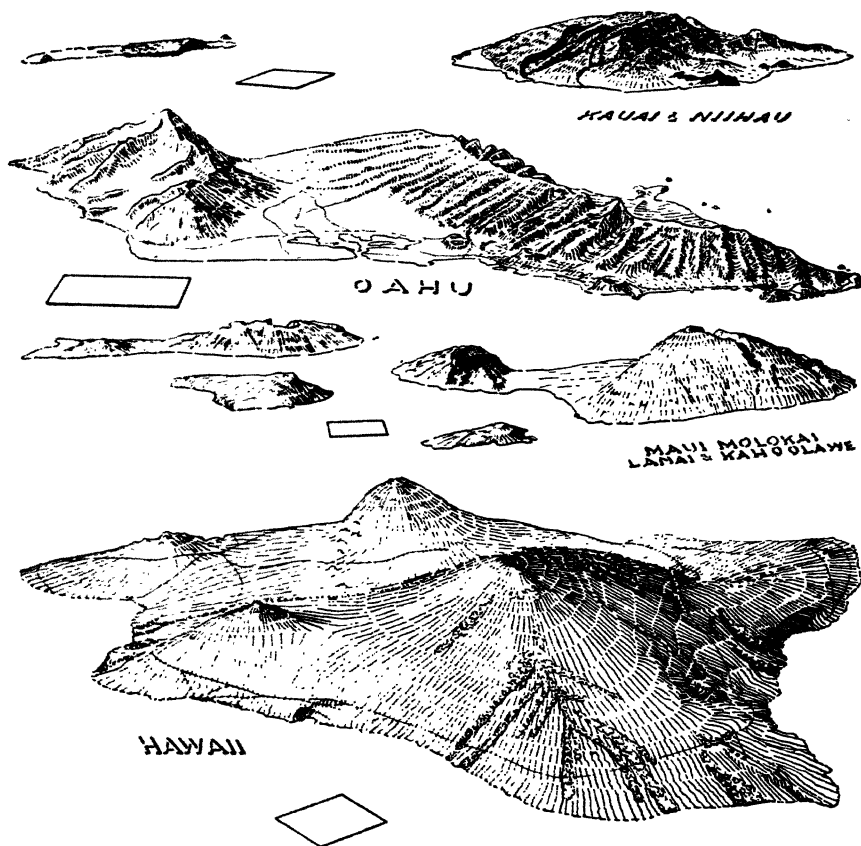


Figure 5.—The main Hawaiian Islands separated into four groups and arranged in perspective. The horizontal scale is indicated by quadrangles 5 miles square. The vertical scale is somewhat exaggerated. (Rearranged from Wentworth, 1939.)

others are much eroded, and still others have worn down to submarine platforms on which grow coral reefs.

Unlike the western Pacific, the eastern Pacific has experienced relatively few changes. Its present depth and position of islands are essentially those of past geologic times. The evidence shows that most Polynesian oceanic islands have experienced uplift and subsidence at different times, at different rates, in different amounts, at different places. So far as known, the extreme range in oscillation is something like 1,200 feet, so that islands now separated by less than 500 feet of water may have been nearly or quite joined, but islands now separated by as much as 1,000 feet probably were not joined, and parts of the sea floor at greater depth doubtless have never felt the air. There is no geographic evidence for greatly enlarged islands, vanished archipelagoes, or "lost Pacific continents."

For the Pacific as a whole perhaps the most significant feature of land distribution is the extension of Asia southeastward through the Malay Peninsula and on through Sumatra, Java, Celebes, Ceram, Papua—five big islands associated with many small islands in such manner as to form nearly continuous land. And beyond Papua as far as Fiji the Ocean is packed with islands. In essence this great region of Indonesia and Melanesia is a suburb of Asia. In age and composition its rocks are those of the continent; its animals and plants predominantly are those which now live or once lived on the larger land mass.

Gulick (1932:421) ably emphasized the disproportionate amount of open sea in the Pacific when he wrote "... any part of the ocean where the proportionate area of fairly deep sea falls as low as 98 per cent, and the area above water becomes as great as 0.2 per cent is treated by geographers as dense archipelago. It is, geologically unlikely, therefore, that this vast area could ever have been actually continuous land, as that would involve a considerable alternation in the isostatic balance of a whole major region of the earth, although faunistic arguments favoring such a supposition have been brought forward..."

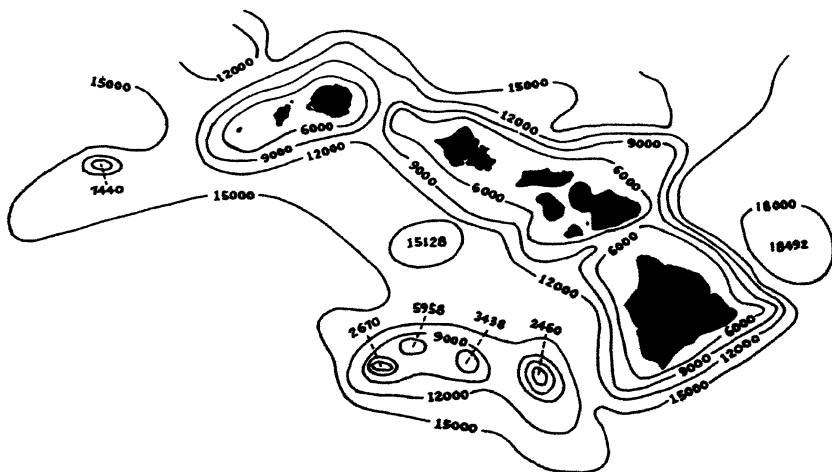


Figure 6.—Submarine contours around the main Hawaiian Islands. Depths in feet.

E. H. Bryan, Jr., has tabulated (in manuscript) the islands of Micronesia, and he has informed me that in the Marshalls, Carolines and Marianas there are 77 coral islands and 20 islands with exposed basalt. These units contain 2,148 individual islands whose combined land area is only 903 square miles, about a quarter of which is made up by the island of Guam alone.

The area of the Pacific is variously given with great discrepancies, but according to one source (National Encyclopedia) the area is about 71 million square miles, or more than the combined areas of the Atlantic (40 million) and the Indian (29 million) Oceans. The average depth of the Pacific is said to be about 15,000 feet. The greatest depths recorded are along the northern and western sides. South of the Aleutian Islands the Albatross Deep is recorded as 24,012 feet. Ramapo Deep, southeast of Yokohama, is 34,626 feet deep. Mindanao Deep, close to the northeast coast of Mindanao, Philippines, is 35,400 feet deep. Aldrich Deep in the Kermadec Island region is 30,930 feet deep. Other "deeps" occur along the South American coast.

According to information given by the U. S. Coast and Geodetic Survey chart 4000, the Hawaiian Island chain from Hawaii to Kure, within about 75 miles on either side of the islands, is surrounded by depths between 15,000 and 17,000 feet. In some localized areas irregularities are indicated. For example, within 30 miles of the east coast of the island of Hawaii a depth of 18,876 feet has been recorded (thus, the continuous slope between the top of Mauna Kea and this deep is 32,660 feet within 60 miles!). Farther out to the south there are depths that exceed 18,000 feet between Hawaii and Kingman Reef. There is no suggestion whatsoever of extensive submarine ridges or banks which might indicate shallow-water connections with any other archipelago extending outward in any direction from any part of the Hawaiian Archipelago. There is positive evidence to indicate that here and there within 500 miles, for example, there are areas shallower than 15,000 feet which are indicative of local volcanic activity that stopped before building any great underwater masses which approached the surface. On the other hand there is said to be a submarine volcanic mass that rises as much as 13,000 feet from the ocean floor about 140 miles SSW of Honolulu. Also, there is said to be a submarine range of "high mountains" about 200 miles southwest of Necker Island. More detailed soundings will reveal additional irregularities. The floor of the central Pacific Basin is studded with hundreds of submarine volcanic masses of varied sizes and elevations which have never felt the air; some of them rise for several thousands of feet above the ocean bottom. This is as we should expect it to be in accordance with the basic theory which governs our present conclusions. It is probable that more adequate mapping of the ocean bottom will reveal that there are many more submarine volcanic cones in the basin than the number whose tops appear above the surface today.

If there were ever continental masses in the true Pacific Basin, various methods of physical measurement would reveal them. The study of seismological data alone brings to light some fundamental facts concerning the Pacific Basin. One need not send equipment to the bottom of the Pacific in order to sample the rock

to know its basic nature. Earthquake waves travel at different rates through rocks of different densities and the differences in speed are indicative of the nature of the rocks. Thus Gutenberg (in Vaughan, 1937 :41-44) notes that the speed of a wave in Recent, unconsolidated sedimentary rock is about 1 km./sec., but in basalt it is 5.00-5.75 km./sec. Using this method of analysis, he found a "difference in structure between the Pacific basin and all other regions of the earth." It was found that

In the Atlantic and Indian Oceans, the total thickness of the crust is only a fraction of that on the continents; ...but in both oceans there still is a well-marked discontinuity between the crustal rocks and the mantle....In the region of the Pacific basin no marked discontinuity

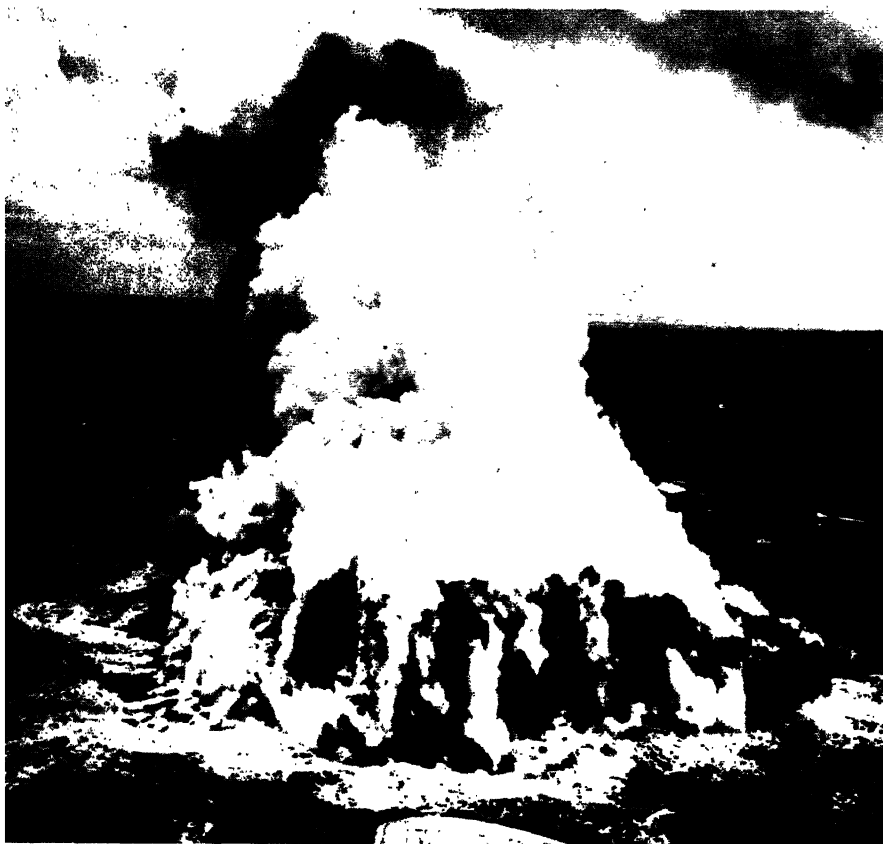


Figure 7.—A new Pacific island building up from the depths of the sea (31 degrees 58.5 minutes north latitude, 139 degrees 57.75 minutes east longitude). Our present Hawaiian Islands may have appeared similar to this when each first appeared above the surface of the sea. (Official U. S. Navy photograph, Pacific Fleet, 1946.)

between crust and mantle exists; except for local accumulations of erupted basaltic material, it does not appear that the elastic constants near the rock surface differ significantly from those of the mantle. . . . It seems to be very probable that the continental layers consist of granite at the top, and rocks with increasing basicity at greater depths, that the bottom of the Atlantic Ocean is formed by the same type of rocks, the layers being noticeably thinner, and that the entire bottom of the Pacific Ocean and all regions of the earth at depths of more than 50 kilometers consist of very much more basic material than is characteristic of the uppermost part of the continents.

The following is Gutenberg's summary:

...we find that the region comprised within the limits of the Pacific Ocean... has one kind of structure and all other regions of the earth, perhaps excluding a part of the arctic basin, another. In these latter parts of the earth (non-Pacific area) there is a continental layer which consists of several shells. Its thickness is about 40-50 kilometers under the continents but decreases towards the Atlantic and probably the Indian Ocean, where its thickness is of the order of 20 kilometers. There is no indication that the continents have broken during any geological time and drifted apart; however, our findings would be in agreement with the assumption that in early geological times the thickness of the continental crust was different in many localities from what it is today and that plastic flow in the continental crust may have changed the distribution of land and sea in the area including all continents and the Atlantic and Indian Ocean.

The basin of the Pacific Ocean proper is a unique element of the earth's crust and its boundaries affect the layers down to many hundreds of kilometers. As it is not evident how the continental crust could have been removed in a gradual way from the Pacific Ocean the conclusion seems to be probable that the Pacific Ocean either never had such a crust or that it was removed by a cosmic event.

Gutenberg and Richter in their paper "Seismicity of the Earth" (1941:82) say, "The Pacific basin is the largest of all the stable masses. Except for the single interval zone of the Hawaiian Islands, and for possible volcanic shocks in some other island groups, it is an area of complete seismic calm. This is particularly well established for the north Pacific."

Fleming (in Vaughan, 1937:52), in discussing magnetic ocean surveys, says that "under the Pacific Ocean the basic surface of the Earth's mantle is practically exposed. There then we may expect different geological and geographical properties from those found elsewhere," and he notes that there is a difference in magnetic variation over the Pacific "as witness the moderate rates of annual change over the Pacific as compared with those over the Atlantic and adjoining continental areas."

Unfortunately, detailed gravity research has not been conducted in the mid-Pacific, but such needed investigation should supply many pertinent facts. The incomplete gravity data available for Oahu indicate that the volcanic mass rises from an unbroken crust. Betz and Hess (1942) quote the following material from the work of Meinesz, who, in discussing gravity anomalies for Oahu, says, "As far as this scanty material allows a conclusion, we have seen that it points to the island being a volcanic load on an unbroken crust. There seems to be no root at the lower boundary of the crust or, if there is one, it cannot have great dimensions, for else the regional anomalies ought to show stronger deviations than

they actually do. So we may conclude that the present material points to a crust which has undergone no shortening at all. This would determine the islands as huge volcanoes piled on the ocean-floor and pressing down this floor by their weight."

Even du Toit, that indefatigable student and advocate of continental drift, evidently finds the foregoing conclusions consistent with his basic ideas of the Pacific Basin. He says (1940:182), "The current idea of a subbasic to basic ocean floor finds support from earthquake waves, gravity anomalies, and volcanicity. . . . The ocean appears to have developed from a larger Mesozoic basin through the pressing-in of its framework in the manner pictured under the hypothesis of drift. . . . The intra-Pacific region remained neutral, though put in slight tension latterly, and is characterized by youthful basalts and nepheline-basalts emitted largely from vents. The circum-Pacific compression girdle is, from the Mesozoic onward, marked by recurrences of andesites and granodiorites."

Betz and Hess (1942) in preparing their recent paper on "The Floor of the North Pacific Ocean" have had available numerous new data including recent gravity studies and results of more than 35,000 sonic soundings made by the

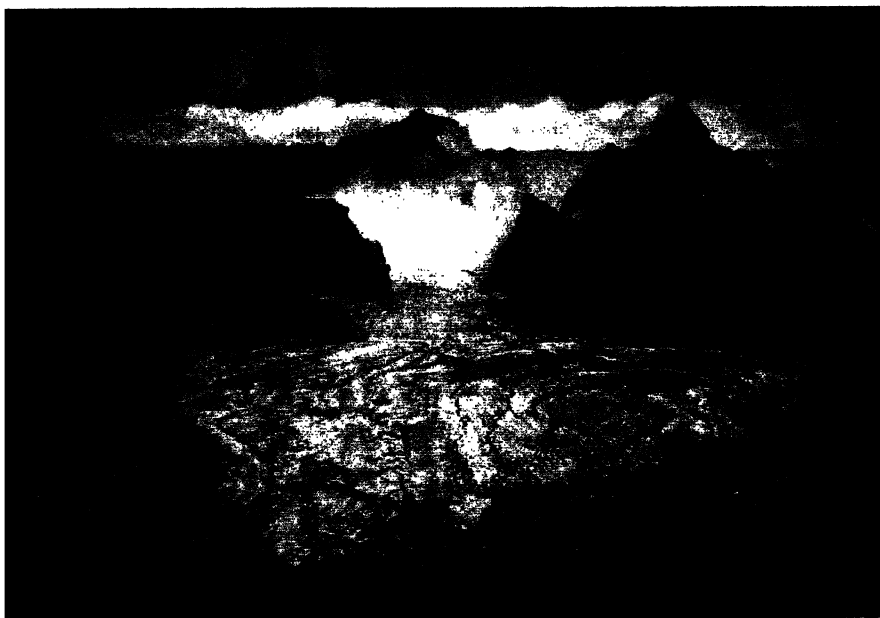


Figure 8.—An example of a principal feature in the upbuilding of the Hawaiian Islands: the outpouring of molten lava at Kilauea. (After Stearns and Macdonald, 1946. Photograph by T. A. Jaggar. Cut loaned by U. S. Geological Survey, Honolulu.)

United States Navy. Their careful weighing of the evidence leads them to conclude that the data now assembled do not support Chubb's conclusions (1934) that the mid-Pacific island chains arise from submarine ridges of fold origin. They agree with Williams (1933) that, if the volcanoes were removed, no submarine ridges would exist. They say (p. 108), "If the volcanic peaks are disregarded, the region of the islands would seem to be a hardly perceptible swell, not a ridge. . . . Considering the probable strength and thickness of the crust, a fold of 600 miles wide (width of the Hawaiian Swell) seems improbable. In cross section, the configuration of the swell does not suggest folding." In place of the fold and ridge theory, Betz and Hess (1942:109) conclude that "A hypothesis that would entail the opening of fissures—perhaps tension cracks—on the floor of the ocean and the extrusion of large amounts of volcanic material to build up the gentle rise of the swell would seem to agree with present observations." Also, in reviewing the conclusions of Chubb, Williams and Powers, Betz and Hess say (p. 110) that "the opening of fissures to permit the extrusion of volcanic material is generally postulated, but the manner in which they developed is not agreed upon." They conclude that "Fissuring and volcanic eruption suffice to account for the Hawaiian Islands and similar island chains in the Pacific Basin. . . ." Chubb (1934:295)



Figure 9.—Islands in the molten lava lake in Halemaumau, Kilauea. (After Stearns and Macdonald, 1946. Photograph by T. A. Jaggar. Cut loaned by U. S. Geological Survey, Honolulu.)

calls for strike faults and dip faults resulting from folding, and moving anticlines to account for the formation of the island chains. Williams (1933:7) suggests that the island chains "are located along lines of fracture, that they represent the summits of great volcanic cones developed on a more or less flat ocean floor by the outpouring of lava from crescentic fissures determined by the outcrop of thrust-planes with the curved surface of the globe." The findings of Betz and Hess do not support those of Chubb, and these authors do not recognize the crescentic thrust faults of Williams in the data at hand. They believe that "Any fault to be considered in the formation of the Hawaiian Swell was probably of such a nature that great vertical displacements did not occur generally along its course. This suggests to us the possibility that the swell may lie in a zone of trans-



Figure 10.—The 1935 flank eruption of Mauna Loa. Photograph by U. S. Navy showing the fiery streams of lava flowing down the slopes. (After Stearns, 1946. Cut loaned by U. S. Geological Survey, Honolulu.)

current, or strike-slip, faults, such as the San Andreas fault [in California], with its dominant movement horizontal. The relative straightness of the Hawaiian trend, as well as of similar island trends in the Pacific Basin, implies that the probable fissures along which the volcanic material ascended were vertical or nearly so." The map prepared by Betz and Hess is significantly instructive.

DERIVATION AND CHARACTER OF THE ROCKS

The rocks of the Hawaiian Islands are derived from two basic sources: (1) basalts or related rocks from the molten magma of the earth's interior; (2) from the deposition of calcareous and organic materials by marine plants and animals. There are also minor deposits of calcareous and siliceous materials from solution. There are no earthy materials naturally present other than these or their derivatives. There are no commercial mineral resources available other than water, building stone, road metal, recent reef limestone, sand and similar products. There are no deposits of gold, silver, copper, precious gems or other such minerals or elements. There are no ceramic clays with the exceptional occurrence of some small, aberrant pockets of almost negligible commercial value found in a few restricted mountain areas. There are no glass-making sands. There is no coal. There are no metamorphic rocks. The rocks are characteristic of average, normal, isolated, oceanic islands.

THE BUILDING OF THE ISLANDS

Because of stresses set up in the earth's crust, a linear zone or zones of weakness developed along the north-west south-east line beneath what is now the Hawaiian Islands. Along this line, great submarine volcanoes burst through the weakened crust and poured forth uncounted cubic miles of lava. Broadly speaking, it appears that it was along the northern part of the line that the magma first broke through. How long ago this process of relieving tension began, no one knows; but it is known that the Tertiary—especially during and since the Miocene—was a period of extensive volcanism, and the beginnings of the Hawaiian Islands probably were during that period of the Cenozoic era. There appears to be no evidence of pre-Tertiary volcanism in the Hawaiian part of the Pacific Basin. At this early part of our discussion, therefore, we have dated the birth of the Hawaiian Archipelago as post-Cretaceous.

By a gradual process, the first islands were built up beneath the sea. Their beginnings were at great depths—between 14,000 and 18,000 feet below sea level. Unless the speed of upbuilding was greatly accelerated during the submarine period, the length of time required for the volcanic mass to reach the surface was far greater than its subaerial activity. This conclusion is obvious, because each of these islands has many times the bulk beneath sea level that it has exposed above the sea. There appears to be no good reason for supposing that the rate of outflow was extraordinarily accelerated at the beginning, although it is probable that it was somewhat more rapid than near the maturity of the volcanoes. The almost universal thinness of the lava flows supports this view.

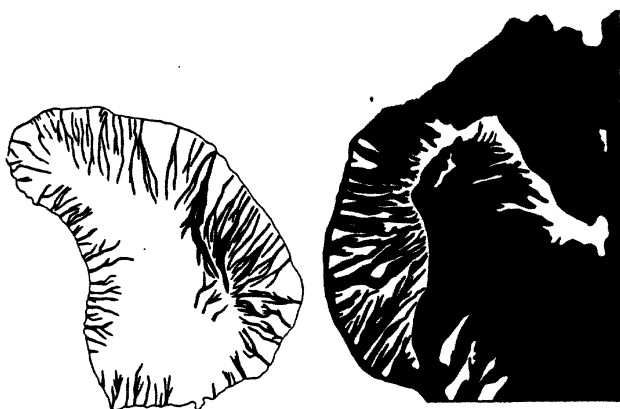


Figure 11.—Maps of comparatively young and old island areas to show amounts of the original surfaces which have been eroded away. The areas from which the original volcanic surface has been removed are shown in black. Lanai, one of the younger of the main Hawaiian Islands, is at the left. The greatly dissected southwest part of old Kauai is shown at the right. (After Wentworth, 1928.)

To some workers, it appears that the volcanic activity, or speed of upbuilding, is greatly retarded at the present time. However, such a conclusion may be misleading. The constructive processes of Mauna Loa during the past century of recorded eruptions indicate that enough material has been poured out of that mountain to raise its dome between three and six feet in one hundred years! It has poured out an estimated five to ten billion cubic meters of lava in the last century. The flow of 1859 added 600 million cubic yards alone. Mauna Loa is so huge that if Mount Rainier, Mount Hood and Mount Shasta in North America were placed within it, there would be space left over for ten more of any one of them, it is said. The smaller, visible part of the mountain contains more than 1,000 cubic miles of lava. If the construction rate of between three feet and six feet per century be taken not as fact but only for the purpose of illustration, a mountain 13,000 feet high could be built in about 225,000 to 450,000 years. The great volcanic mass that is the island of Hawaii appears to be the product of about a half a dozen separate major conduits whose combined action may have resulted in the construction of the mountains of that island in less eruptive time. On the basis of estimates of upbuilding of island areas in Hawaii, it is suggested that the constructive period for a 13,000-foot mountain might conceivably be as rapid as 45,000 or even 22,500 years! (But I am not intimating that such a spectacular speed has been attained, although it is theoretically possible.)

The history of Falcon Island in Tonga has been fairly well recorded, and a few notes taken from the United States Hydrographic Office "Pilot" no. 166, vol. 2, 1933, regarding it as an example of rate of growth may be of interest and not altogether out of place here. The island was discovered in 1865 as a reef;

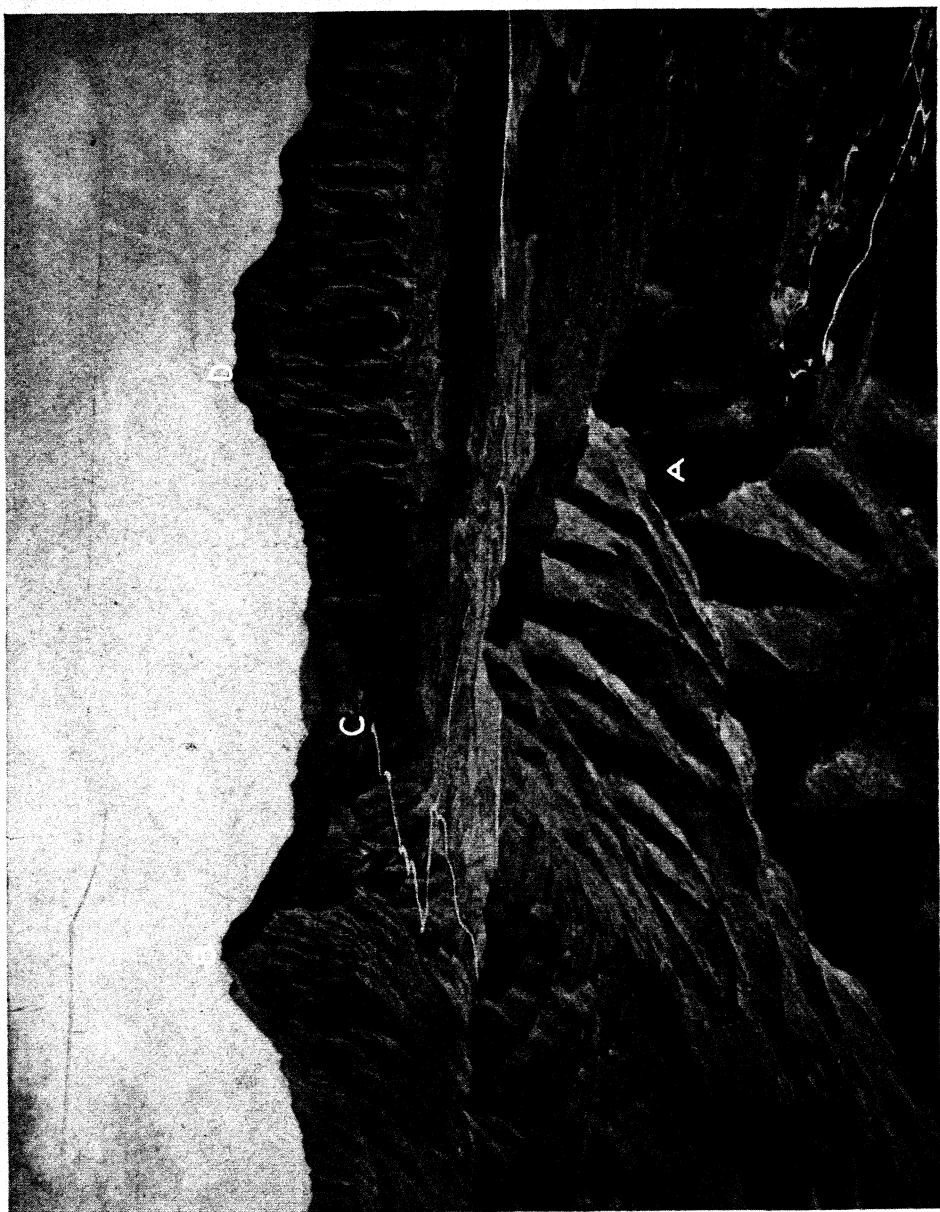
it was seen as an island above water in 1885; in 1889 it was 1.3 miles long, 1 mile wide and 153 feet high, and was estimated to have been two-thirds washed away since 1885; in 1894 it was almost entirely washed away; in late 1894 it was found to be 3 miles long, 1.5 miles wide and 50 feet high; in 1898 it had washed away again to a shoal about 100 yards long; in 1900 it was 9 feet high; in 1913 it was under water; in 1921 there were about 3 feet of water over it in its shallowest part; in 1927 it was steaming and found to be 1,739 by 1,430 yards in extent; in 1928 it was in eruption and reported to be about 2 miles long, 1 mile wide and 600 feet high; in 1930 it was reported to be about 1.2 miles long and 475 feet high. The average rate of growth between 1921 and 1928 was about 86 feet in elevation per year. However, this island is composed of cinders and ash, and its growth rate must be interpreted in the light of that fact.

There have been recorded enough soundings, around our main islands at least, to enable us to understand the gross underwater contours and extent of the islands. Each is a typical volcanic dome arising either from the floor of the ocean or breaking through the underwater slopes of a neighboring island. Their base is the floor of the sea—not an underwater platform which in any way can be called a “continental” type. However, the main islands are so close to one another that their bases have merged and all are united at depths from a few hundred feet, as between Maui, Kahoolawe, Lanai and Molokai, to more than 11,000 feet between Kauai and Oahu. They are true oceanic islands.

DEGRADATION OF THE ISLANDS

As soon as the islands were built, submarine and later subaerial activities—chemical and mechanical—began to tear them down. At the beginning, the rate of construction exceeded that of degradation and the islands rose out of the sea. However, as volcanism abated, the less spectacular but nevertheless gigantic forces of erosion took the forefront, and, with the exception of only parts of the island of Hawaii building up with its contemporary volcanoes, these islands are in the process of being torn down and flung back into the sea. In fact, most of the leeward islands have been completely worn away and have suffered subaerial removal as well as being cut off as far below sea level as the action of the waves and currents could abrade their tops, or they have been submerged to lower levels by subsidence of the land or rise in sea level. But some of those islands have entered into another constructive phase—a biological one—for today they are capped with coralline products. Again they have risen out of the sea as the waves have torn at the reefs and hurled the plant and animal skeletal and shelter material as high as the limit of storm action or tsunami (“tidal” waves), and winds have swept it farther upward. However, unless and until volcanism should break out in them again, or until they should rise in relation to sea level by diastrophism or climatic change, they are doomed to eons of time in the monotonous existence that is the fate of atolls.

These processes are not ended; they are in continued full force all around us. The land upon which we now stand is by natural law willed to the sea. Eventually,



all these majestic islands will meet a similar end—a burial at sea and a headstone of biological lime.

RATE OF DEGRADATION

The speed of erosion is the direct result of the action and combination of the destructive forces and the nature of the substratum involved in the given region. Weathering in the Hawaiian Islands needs to be interpreted in the light of the special conditions characteristic of the islands.

The topographic features of the islands above marine action are principally the results of chemical and fluvial erosion acting upon particularly susceptible strata. The bedding of lava flows of different porosity and resistivity, the enclosed lava tubes, cracks and weak zones, together with the other characteristics of the mountains, make for unusual permeability and are of major importance in the denudation processes and results.

In the words of Wentworth (1928:385,387) the erosional features of the islands

... are mainly the product of the normal erosional processes of the region, of which the conditions differ somewhat markedly from those of most temperate, humid, parts of the earth. The principal factors are the high porosity of the rock and its susceptibility to chemical weathering, the high mean annual temperature and the rarity of great ranges of temperature, the absence of frost and the high annual rainfall of certain parts of the group. As a result, chemical weathering at elevations near the low water table dominates the development of the deeper valleys and is a controlling factor in determining their configuration.

The major structure of the rocks of the Hawaiian Islands is simple and uniform. The entire land mass above sea-level is made up of thin basaltic flows lying one on another to form cones some of whose bases are as much as 40 or 50 miles in diameter and whose summits rise to maximum elevations of nearly 14,000 feet above sea-level. The submarine dimensions of the cones are enormously greater. The individual lava flows are in the main from 5 to 20 feet thick, very few so far as known exceeding the latter figure over any considerable area. Most of the individual flows are limited to one side of the cone of which they form a part, and, in general, probably have a width of considerably less than the radius of the cone. The lengths of the flows vary from a few yards up to a few miles, and the areas of historic flows on the island of Hawaii range up to 20 or 25 square miles. It is apparent that unless the old flows which have formed the various islands were of far greater extent than the historic ones, there are great numbers of slight unconformities between over-lapping flows, but the exposures are so limited and the identification of key flows so difficult that the structure gives the impression of great uniformity and parallelism.

EROSION

Because of the tropical climate, frost action is a negligible factor in the degradation processes over the islands as a whole and is significant only on certain of the highest peaks (see section on glaciation). Eolian erosion probably had little

Figure 12.—An extensively eroded landscape—the precipitous Nuuanu Pali, Koolau Mountains, Oahu. According to some investigators, Kokokahi Peak (A, in the foreground) is a root of the ancient firepit of the Koolau volcano. The highest peak in this range is Konahuauui, 3,105 feet, at B; Lanihuli is at D, and the Pali gap at C. (After Stearns, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)

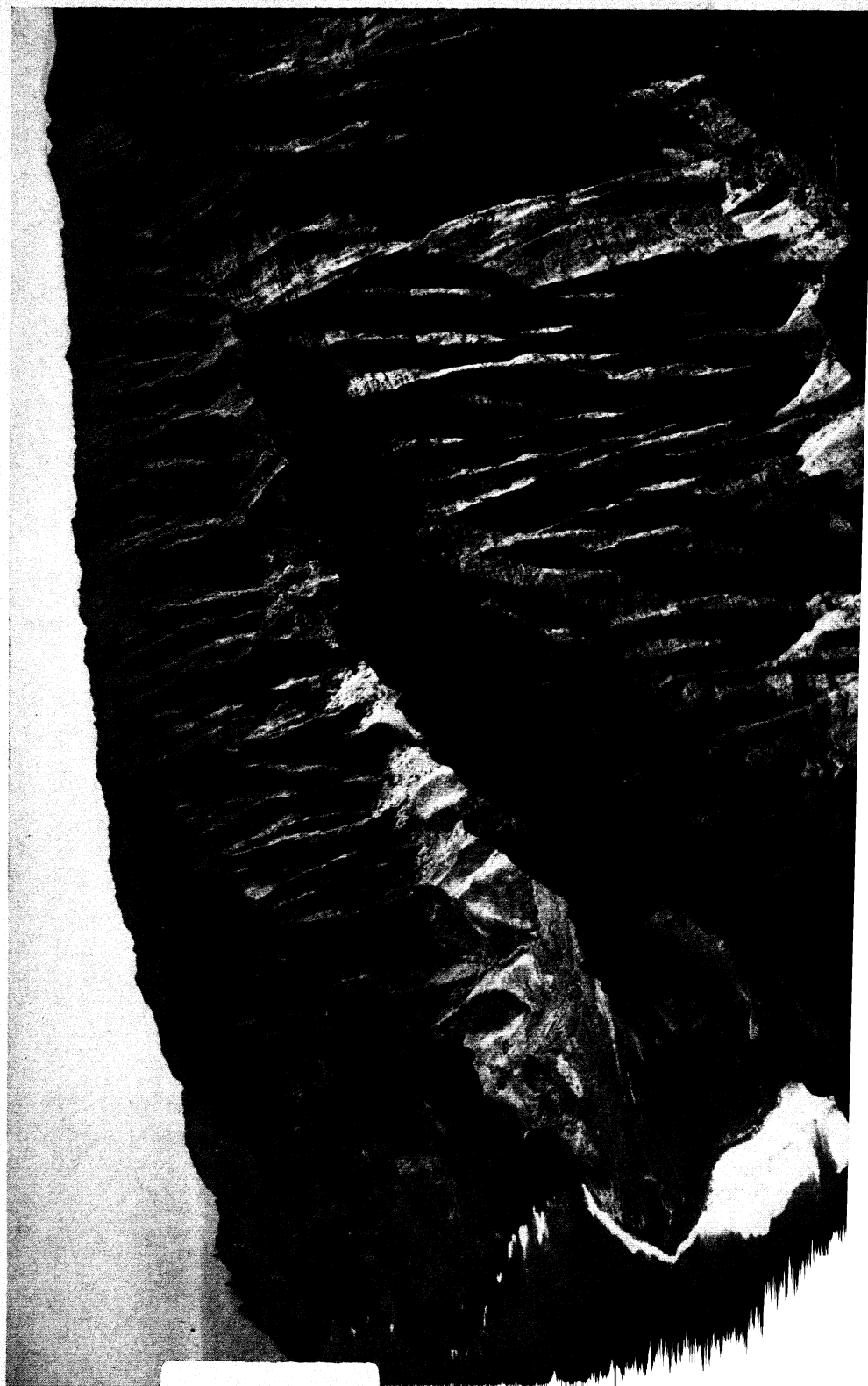
to do with the principal erosional features of the islands before the advent of man and, more particularly, his grazing animals. However, the overgrazing of the dry island of Kahoolawe has resulted in an island that has been blowing out to sea for many years. Therefore, chemical, marine and fluvial erosion, together with the action of plant growth, are to be regarded as the prime factors of erosion in prehistoric Hawaii.

The sea and land have shifted and reshifted in reference to one another, and the attack of the sea at any given temporarily stable level has not been geologically great. There are peneplains on the windward sides of the older islands. Evidence is widespread around the seaward parts of the islands to show conclusively that much marine erosion has taken place. It appears reasonable to believe, therefore, that the soundest approach to the subject of erosional time would be based upon subaerial erosion and the comparative amounts of material removed.

There are a number of special conditions in these islands which account for their characteristic topography. Of these, the nature of the rocks, their composition, porosity, reaction to mechanical and chemical weathering, structure and formation are contributing parts, but there are other factors. One of the most important is the climate. Owing to the heights attained by the main islands, the mean rainfall is great (about 100 inches for the entire group). Also, in certain areas exceptionally wet conditions are the rule. On Mount Waialeale on Kauai (elevation 5,080 feet) the average rainfall is the greatest recorded over a period of years of any place on earth. The mean annual rainfall for a 30-year period to 1942 was 462.7 inches, but the more complete and accurate records for the 12 years between 1930 and 1942 show an average of 537.5 inches per year. In the year ending July 24, 1942, 618.75 inches (51.56 feet!) of rain were recorded. However, only 15 miles away from that rainfall station is a lowland one whose annual mean is between 15 and 20 inches. On the island of Maui a station at 5,000 feet recorded 562 inches of rain one year, and a lowland station only 8.5 miles away recorded as little as 2.5 inches for one year. These large amounts of water falling in the highlands have left a spectacular topography in their wake. Moreover, much of the weathering and erosion here may be compared to that of limestone areas: this is a significant feature.

Unlike the water table of much of the continental United States, for example, the water table in Hawaii does not cling close to the topographic outline of the land, but is deep down and is controlled by the character of the rocks, the depths of the valleys and the saturation of the lower rocks with sea water. Wentworth's figures (1928:395) graphically present this and are reproduced here (fig. 15). Stearns (1935:236) found the water table to slope from 1.6 feet to 3 feet to the mile in certain sections of Oahu, and said, "Such flat gradients are also charac-

Figure 13.—Waimea Canyon on Kauai. This great canyon is cut through 3,500 feet of old lava flows and runs from an area of extremely heavy rainfall to the dry coast of the island. The area in the foreground is dry and has been extensively grazed over, especially by goats. Note the bedding of the lava flows, particularly in the background. (After Stearns, 1946. U. S. Navy photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



teristic of the basal water table in the other islands and indicate that the rocks are exceedingly permeable."

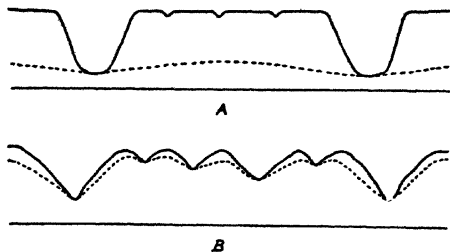


Figure 15.—Diagrams of water tables to show the relation of ground water to the topographic surface in Hawaii (A), and the same relation in a humid part of the United States mainland (B). (After Wentworth, 1928.)

The chemical weathering that accompanies heavy rainfall and the subsequent dense vegetation cover is, according to Wentworth, the paramount weathering activity. The low water table results in the most active weathering not upon the heights, but low down near the water table. This conclusion is the reverse of what many casual observers are likely to believe, but is ably elucidated by Wentworth. Thus the rugged topography of the islands is produced by these special and, to many observers, cryptic processes. Wentworth (1928:396) says:

The greater activity of weathering near the water table and hence at low altitudes, and the capacity of the rock partially weathered chemically to stand at high angles when physical weathering is inoperative, combine to produce slopes of great uniformity and steepness. The declivity of the slopes is the angle of stability for the unweathered or moderately weathered material of the cliffs. The uniformity of steepness to the very top of the slope is a result of nearly uniform wastage from the base of the cliff, either by weathering or by stream transport. In most regions [continental] the upper parts of slopes are affected by weathering processes of a type which are progressively more active at higher altitudes, and the higher slopes have also been longer subject to such action. Both of these factors tend to produce gentler slopes at the top of any given profile and hence convexity of the upper part of the profile. On the contrary, agencies which are more active at lower levels are responsible for the forms of the deeper parts of valleys which are of necessity concave. In most parts of Hawaii the processes which promote more rapid wastage at lower levels are dominant, and the wastage at the lower levels is shown in the nearly uniform slopes of cliff faces.

Many readers will immediately recall that these conclusions are the reverse of the classroom principles of geology which they received in their continental university or college training. Valleys which might be classed as glacial valleys in North

Figure 14.—Looking northeast along the Napali Coast of Kauai (the large valley is Kalalau), showing the erosion patterns typical of some of the wet, seaward faces of old areas. Note the gentle slopes of the ancient lava flows, best seen toward the top of the ridge in the foreground. The ridge in the background rises to more than 4,000 feet at the right. The sea cliff is about 2,700 feet high. I need not emphasize the difficulties one encounters in attempts to explore this type of terrain. (After Stearns, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



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America are normal products of chemical and fluvial erosion in Hawaii. Conditions on Pacific islands are not the same as those existing in North America or Europe and they must be studied geologically and biologically with this fundamental point constantly in mind.

Stearns's theory (1935:24) is based upon "(1) the original slope of the surface, (2) the presence of alternating resistant and nonresistant beds dipping downstream, (3) high rainfall at high altitudes and low rainfall at low altitudes on a conical surface, thereby inducing active piracy in the upper parts of the drainage basin and (4) plunge-pool action and landslides removing the divides between tributaries."

A combination of both these points of view is justified; there are many factors which must be taken into account. Some of these are the rapid disintegration of the basaltic lavas as a result of the acids released from large accumulations of decaying vegetation of the dense rain forests; the weight of masses of vegetation on steep slopes, the common resultant landslides and the great spalling effect they have; the rapidity of stream erosion on the steep slopes; the large numbers of waterfalls; the spectacular cutting through of mountain ranges and stream piracy. The spalling effect of landslides appears to play a dominant role in the configuration of higher slopes. Landslides may tend to form new water courses which may, in part, influence the spectacular fluting of cliff areas and steep slopes. Forbes (1885:115) was struck by the action of landslides in Java and wrote,

During the rainy season the thunder of slopes laden with forest trees and shrubs crashing down, often for hundreds of feet into the valleys, was a daily sound, which impressed me with the supreme potency of rain as an agent in planing down the mountains and widening the valleys. I have often been astonished at the rapidity with which even a small stream will carry away the *débris* of a great landslide. When a heavy gale accompanies continued rains, the fall of giant trees on the narrowed ridges of mountains is very often the cause of extensive landslips into both the adjacent valleys, which lowers down by very perceptible degrees their barrier ridges.

More emphasis needs to be placed on the action of plants in mechanically breaking up the rock by their root growth. The mass action of a dense rain forest in breaking up rock, thus enabling the resultant soil and finely broken rock to be carried away more rapidly by fluvial means, is enormous.

Since this was written, Wentworth's paper on soil avalanches (1943) has appeared. He concludes that the knife-edged ridges so characteristic of our topography are formed largely by slides. He concludes (pp. 62-63) that

If 1 foot be removed from one slide area and if the next slide be assumed to consist of 1 foot of nearly loosened decomposed rock from beneath it, a slide every 1000 years in each spot would be rapid erosion. In checking over possible rates, it is thought that in the past 8 years,

Figure 16.—Head of Honokohau Canyon, West Maui, 2,300 feet deep, nearly captured by Waihee Canyon (1); Puu Kukui (2) is the highest and wettest peak on West Maui; the pale-colored flats (3) are peat bogs. (After Stearns, 1942. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



in an area of about 15 square miles, in the part of the Honolulu watershed best known to the writer, there have been the equivalent of 200 slides involving an acre each. If it can be assumed that the material removed is eventually carried downslope and to the ocean by streams, the removal of 1 foot of average thickness from these areas is equivalent to a rate of about 1 foot in 400 years for the whole area. Even if these assumptions favor too high a rate, the process can be very significant in land reduction.

GLACIATION

A unique feature of Hawaiian geology is the glaciation of the great mountain, Mauna Kea. On this mountain is displayed the only evidence of glaciation on any island of the Pacific Basin. Interested readers are referred to the detailed accounts of the study of the ice action on the summit of Mauna Kea by Gregory and Wentworth (1937), Wentworth and Powers (1941), and Stearns (1945).

The final story of the glaciation of Mauna Kea has not yet been told, and geologists are not in agreement as to the age and extent of glaciation. The most recent study has been made by Stearns (1945), and he concludes that the top of the mountain is all of late Pleistocene or Recent structure, and that there was a small ice cap present which extended down to about the 10,500-foot level in the most recent glacial epoch—the Wisconsin—about 25,000 to 30,000 years ago. The ice cap which might have extended over about 20 square miles of the summit and reached a possible thickness of 150–350 feet was smaller in extent than the present-day ice cap of Mount Rainier (45 square miles) in the state of Washington.

It would not take much lowering in the mean annual temperature to bring about permanent snow fields on Mauna Kea today. Freezing temperatures are thought to occur there every night in the year, and during some years snow lies on the ground in patches throughout the year. It was estimated by Stearns that if the mountain were extended upward an additional 1,000 feet or more, the permanent snow line would be at about 14,000 to 15,000 feet today. Known shifts in sea level that are now recorded in the seaward parts of the islands probably played a part in the formation of the snow and ice fields.

INFLUENCE OF GLACIATION ON THE BIOTA

The ice age apparently played a more important part in influencing the marine than the terrestrial life of the islands. Reef-building corals grow in Hawaii in a narrow and critical temperature range. It is thought that if the mean minimum water temperature should drop 3° C. or more, the reef-building corals could not flourish. The drop in temperature during the Pleistocene is considered to have been 3° to 10°. Therefore, Gregory and Wentworth conclude that while "Mauna Kea was capped with ice the waters about its base held no reef building organisms." Anyone who has seen the flourishing coral reefs that grow on many islands

Figure 17.—Halawa Valley, Molokai. (After Stearns, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



Eke

nearer the equator, realizes that the Hawaiian reefs are not growing in optimum conditions even at the present time. However, the decadent condition of at least some of the Hawaiian reefs is evidently correlated with food supply, water pollution and recent changes largely brought about by the influences of man.

As Vaughan (1910) points out in his study of Hawaiian corals, "reef corals can endure a range in temperature from 68° F. to 85° F., but the annual mean must not be below 70°; the summer temperatures would be higher. The lowest summer surface temperature recorded by the 'Albatross' was 73°.... The greatest abundance of forms is between temperatures 73° and 78°, depth 0-40 fathoms; ... All the strictly reef building genera live at a temperature of 73°-78° F." Vaughan found that 77 of 121 species of Hawaiian corals studied lived in the 78° to 73° F., 0 to 40 fathom, zone. The number of species dropped to 19 in the 73° to 60° F. zone. Vaughan also notes that the Hawaiian reef fauna exhibits a peculiarity worthy of further notice, in the absence of some of the common reef-building genera of other areas. "There are no species of *Oculinidae*, *Eusmiliidae*, or the *Astrangiidae*; there are very few *Orbicellidae*, none of the large, massive, meandrinoid *Faviidae*, nor of the *Mussidae*."

"The known rate of coral growth shows that post-glacial time is ample for the building of Hawaiian reefs, and also the much greater barriers and fringing reefs about tropical Pacific islands." (Gregory and Wentworth, 1937:1740).

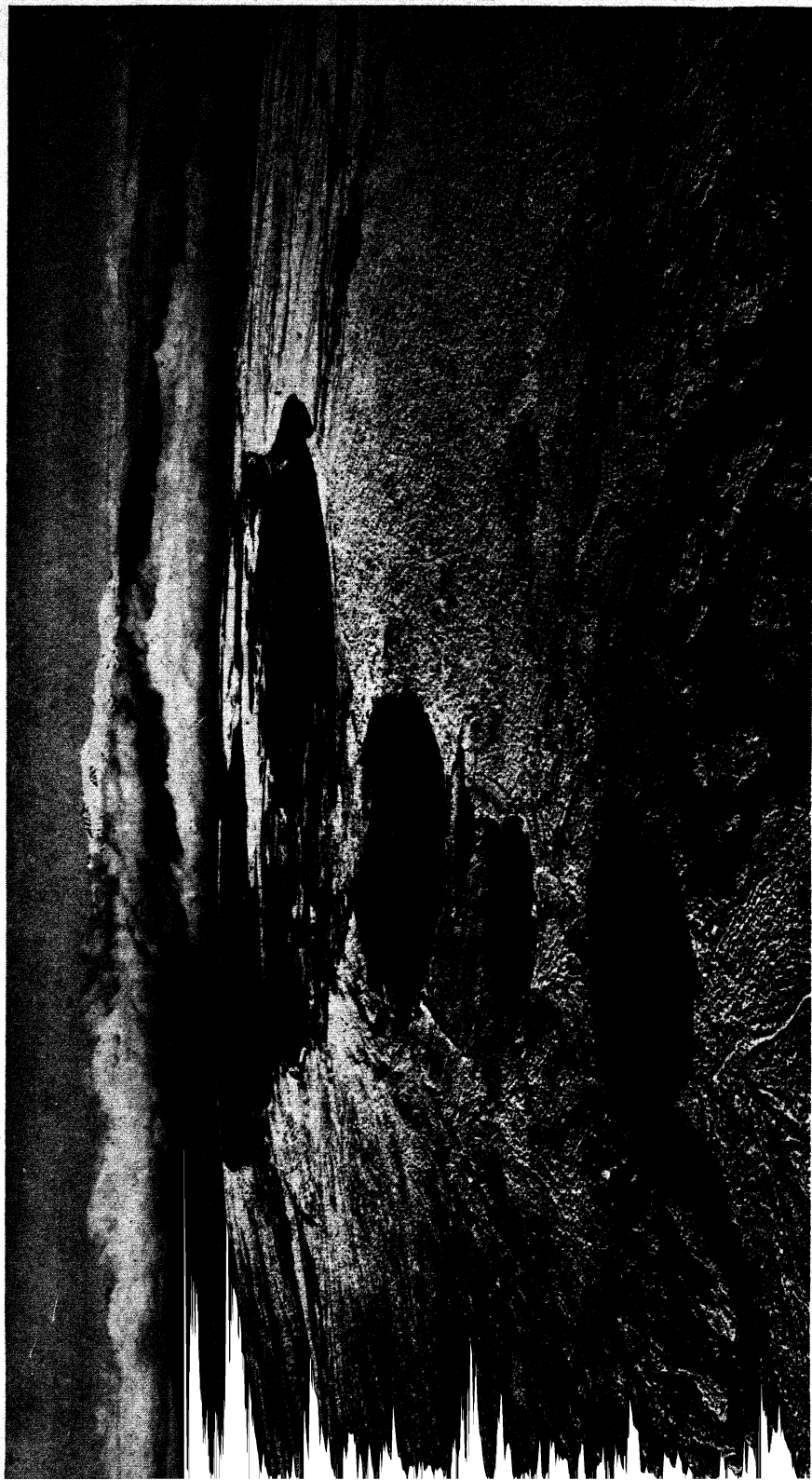
Ostergaard (1928:32) speaking of marine Mollusca said,

In view of the fact that many species now found thriving best in the warmer Indo-Pacific are represented in Hawaii by fossils only and others by species on the border of extinction, it is reasonable to assume that at the time when the limestone of Oahu was formed Hawaii had a higher ocean temperature. A more prolific representation of fossil than of living *Madreporarian* coral on the reefs of Oahu supports this conclusion. Worthy of note also is the presence of well developed coralline algae, which form compact encrusting layers over dead coral boulders and substantially aid in reef building by preventing a breaking up or dissolution of these coral boulders. The efficiency of these corallines in reef building is well exemplified in the reef at Apia, Samoa, where these algae are seen to encrust and cement together coral masses into a firm compact reef, forming a barrier about a mile from shore.

He also states that "On the basis of percentage of extinct forms a geological age greater than the Pleistocene should not be assigned to the emergent limestones of Oahu."

It is probable that the glacial stages in Hawaiian geological history did not have the same drastic influences on the terrestrial flora and fauna that they are thought to have had on marine forms of life. Plants and animals have the ability to move upward or downward or sideways along mountain slopes and can more

Figure 18.—Mount Eke, 4,500 feet high in the wet mountains of West Maui. Its top, about one-half mile across, is a cold, windswept boggy region, with an average rainfall of about 250 inches a year. The mountains in the background rise to 5,788 feet, and rainfall up to 523 inches has been recorded there in one year. Under the clouds in the background the rainfall is only about 20 inches per year. (After Stearns and Macdonald, 1942. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



or less choose more favorable environments, within limitations, during times of climatic changes such as those which have taken place on Hawaii. The zone of local migration of reef organisms is, however, a greatly restricted one, and the effect of climatic change is amplified. It is difficult to ascertain how the colder climate affected the Hawaiian terrestrial biota as a whole. There appear to be no markedly significant features about it that can be attributed conclusively to climatic change within the islands. During glaciation, however, precipitation over the islands may have been greater than at present, and the rate of erosion may have been increased with its consequent influence on species formation as discussed below under Geographical Metamorphosis and Evolution. Today insects follow the plants to tree line and above with no apparent ill effects, and we find "tropical" forms living in regions of frost and snow and apparently getting along as well as those found at middle elevations. However, it is common knowledge that dead insects can be seen by thousands on the barren, wind-swept, arid, mountain-top deserts of the highest peaks where they have been driven from lower elevations by winds and have perished on snow fields or by freezing in those unprotected places. There is nothing in the character of the fauna to indicate large-scale climatic extermination or long-maintained cold climate.

SUBMERGENCE AND EMERGENCE

There is abundant and indisputable evidence of considerable shifting of sea level in relation to land surface in the Hawaiian Islands. The data of such movements have been assembled from the logs of wells sunk to as much as 1,500 feet below sea level, from exposed fossil reefs, from dunes, sandstone, marine-worn boulders, ancient shore lines, well shafts above sea level, drainage canals, road cuts, quarries and similar sources.

The evidence at hand shows that Oahu, at least, now has a sea level in the neighborhood of 1,000 feet higher than it was during earlier periods of its life. Data from wells and the extent to which subaerially cut valleys have been filled or drowned amply support this conclusion, and geologists are in agreement on this point. It is of interest that Recent fossil forest trees have been uncovered in tunnels extending below sea level on Oahu. Also, there is evidence to show that a number of Recent fluctuations of small magnitude have moved the shore line above and below its present level several times over. Because of isostatic balance, major shifts of sea level on one island safely may be assumed to have occurred also on the other islands of the main group, because, except for possible local minor fluctuations of relatively small magnitude, the main group of islands apparently acts as a unit in large-scale movements, and it cannot be considered that any one island has ever acted in major shifts independent of the entire

Figure 19a.—Summit of Mauna Loa after a flurry of snow showing Mokuaweoweo Caldera and pit craters on the southwest rift and Mauna Kea in the background. The highest elevation in the foreground is 13,679 feet. Note the dark lava flows in the foreground. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut courtesy U. S. Geological Survey, Honolulu.)



anastomosed mass. Similarly, the drawing away or adding of water during glacial or interglacial epochs would result in sea-level marks at similar elevations on all of the islands (provided, of course, that they were all above water at any given time). It is significant that the known or postulated shifts in sea level in Hawaii are dated as Pleistocene.

The maximum suggested emergence of any island in the Hawaiian group is indicated by a shore line described by Stearns (1938:618) at about 1,200 feet above the sea on Lanai. According to Stearns, an outcrop of fossiliferous marine limestone is "in place" at an altitude of 1,069 feet, and he says that in his opinion there is no reason to believe that the material has been man-carried to the locality. These marine fossils are recorded from a site at an elevation greater than recorded for any other such Hawaiian fossils. Stearns says,

Evidently considerably more limestone formerly cropped out at this place, but weathering and livestock have nearly destroyed the exposure, leaving only the vein-like deposits. These outcrops are only a quarter to half an inch wide and 2 to 3 feet long. They contain, however, distinctly recognizable coralline algae and gastropods. Some fragments of coral are discernible. Paul Bartsch and H. A. Rehder, of the United States National Museum, found one pelecypod—*Pinctada* sp.—and three gastropods—*Modulus tectum* Gmelin, *Triforis* sp. and *Strombus hellii* Rousseau—in fragments of fossiliferous limestone from this locality. All these forms are now living in Hawaiian waters, which fact indicates that the deposit is probably not older than Pleistocene.

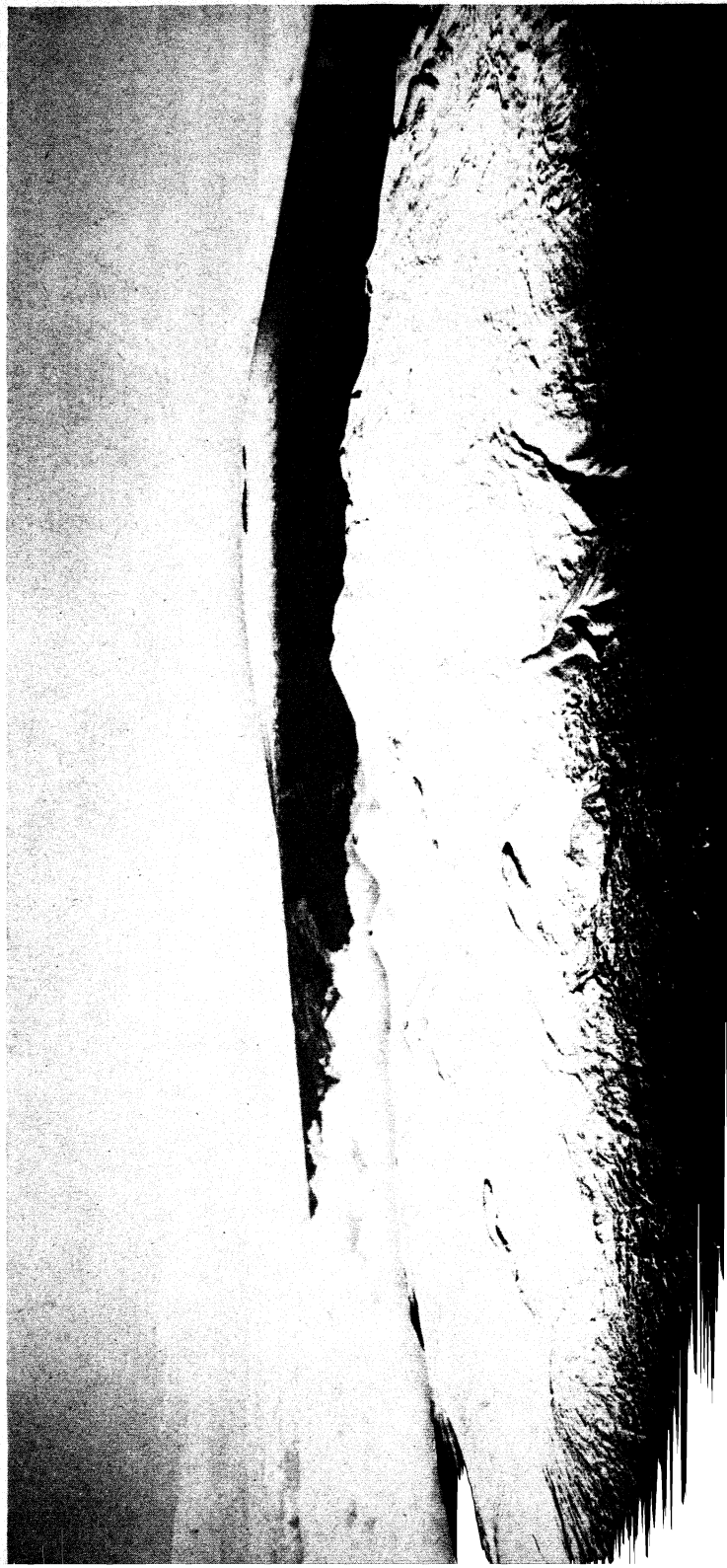
According to Stearns, unstudied indications on Oahu, Molokai and West Maui suggest to him that these islands may also have remnants of an ancient shore line at about the 1,200-foot level which may correspond to that found on Lanai. Other geologists have evidently not seen such indications.

Wentworth's survey of Lanai was made about ten years prior to Stearns's researches, but Wentworth did not find the highly elevated indications of prior stands of the sea that were recorded by Stearns. He says (1925:33),

Coral fragments and shells are found widely spread over the central plateau in association with Hawaiian stone artifacts, but these are clearly of human distribution. In a talus mass at a place northeast of Manele and about 150 feet above sea level shells and coral fragments were found to be so abundant that a natural origin seemed reasonable. Subsequent search in other gulches failed to reveal similar evidences and I have concluded that the deposit must be in part of artificial origin. It is impossible to believe that the sea has stood more than 10 to 15 feet above its present level at any time since Lanai was formed. Had it done so, it seems certain that there would be clear indications at more than one place and of more than one sort.

Such opposite points of view are surprising and somewhat discouraging to the biologist seeking knowledge of the land. Of course, small outcrops of fossiliferous materials might easily be overlooked by the pioneer observer of the gross geology

Figure 19b.—Lava flowing from fissure along the southwest rift at the top of Mauna Loa, April 8, 1940. Note the lava river cascading into the pit crater and the irregular courses of the other flows. Snow lies in depressions in the older lavas. (After Stearns and MacDonald, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



of such a region, but later on may be pointed out to a specialist who can develop an entirely new interpretation after getting a cryptic key to his special field of interest. However, the interpretations given by Stearns evidently have yet to be verified by other geologists. It is regrettable that our knowledge is in such an incomplete stage. For the present, we must give due consideration to the findings of more than one geologist regarding such great shifts of sea level. Moreover, we must not overlook the activities of the old Hawaiians who carried coral and other beach material high into the hills to build their shrines. Materials from the beaches have been carried up the sides of Haleakala, Maui, to about 9,000 feet and used as building material for shrines. Also, ethnologists and others report an abundance of shells and coralline materials scattered over wide areas in the uplands of Lanai—the results of the activities of the Hawaiian people. The Lanai record should be checked carefully. The Hawaiians might have carried coral to the area several hundred years ago, and its subsequent change and burial may make it appear to be “in place.”

Assuming, for purposes of argument, that the more recent estimate of Stearns might be approximately correct, and that there might have been a stand of the sea at about 1,200 feet above present sea level, what influence upon the extent and relative positions of the islands would result? And, on the other hand, what were the results of the downward shift of sea level to about 1,000 feet lower than it stands today?

EFFECT OF SUBMERGENCE

If the sea stood 1,200 feet higher than its present level (so that the lower 1,200 feet of the main islands' present subaerial topography were drowned), roughly about 40 percent of the combined areas of the main islands would be drowned. It would result in all of the main islands being separated by wider channels of ocean than now separate them, but, surprisingly enough, the distances between any two islands would be increased by only a few miles. The greatest increase between any two islands would be between Oahu and Molokai, and that increase would amount to about five or six miles. The flooding of the lower 1,200 feet would result in the dividing of the islands of Oahu, Molokai and Maui each into two islands. Thus, on Oahu the Koolau Mountains would be an island separated from the Waianae Mountains island by a channel about three miles across at its narrowest point at the north, to about eight miles across at its broadest point at the south, and the shallowest part would be about 250 feet deep (the Koolau island would be nearly twice as long as the Waianae island). Molokai would be split into east and west islands separated by a channel about 775 feet deep at its shallowest part and about nine miles broad at its narrowest point, but the west island would be only about two or three square miles in area and only about 150 feet high at its highest point. Maui would be split into east and west islands

Figure 20.—A view of the snow-covered summits of Mauna Kea (foreground), 13,784 feet, and Mauna Loa (background), 13,679 feet. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)

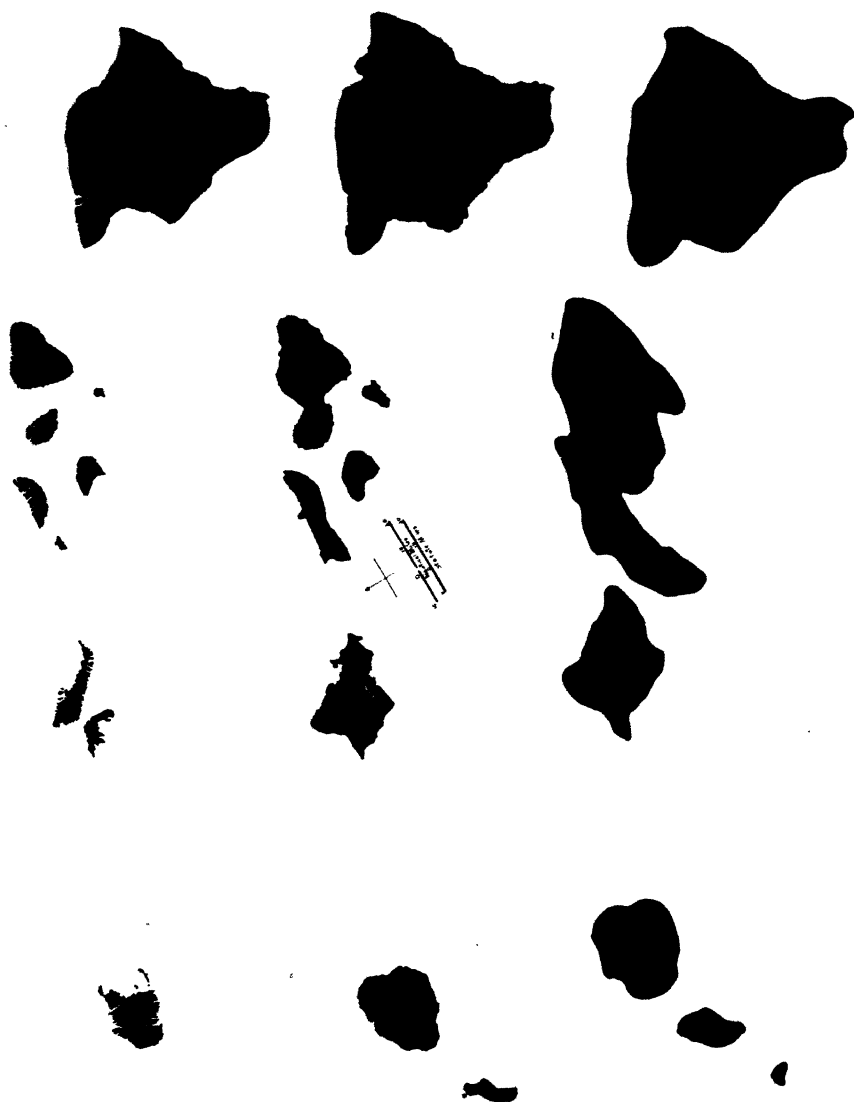


Figure 21.—The middle figure shows the main Hawaiian Islands at the present stage of level of the sea. The top figure illustrates the islands at 1,000 feet above present sea level. The lower figure indicates their appearance at 1,000 feet below present sea level. View figure from side.

separated by a channel about 1,075 feet deep at its shallowest part and about 10 miles wide at its narrowest point. Kahoolawe and Niihau would be reduced to small rocks.

A present-day submergence of between 125 and 200 feet would divide Maui into two islands; submergence of 425 to 500 feet would separate Molokai into two islands; and submergence of 950 to 1,000 feet would divide Oahu into two islands.

EFFECT OF EMERGENCE

An emergence of 1,000 feet would have a greater effect on the area and disposition of land than has been indicated by an analysis of the results of submergence to 1,200 feet above present sea level. The total dry land would approach twice what it is today (about 11,100 compared to 6,435 square miles as determined by rough planimeter measurements). All the islands would be larger and closer together, and Molokai, Lanai, Maui and Kahoolawe would all be anastomosed to form one large island about eight-tenths as great in area as the present island of Hawaii. Niihau would be separated about 10 miles from Kauai with more than 1,000 feet of water in the channel; Kauai would be about 55 miles from Oahu with more than 10,000 feet of water in the channel; Oahu would be five or six miles from Molokai with more than 1,000 feet of water in the channel; Hawaii would be about 18 miles from Maui with more than 3,000 feet of water in the channel.

THE AGE OF THE HAWAIIAN ISLANDS

The dating of these islands in numbers of years is difficult, if not impossible. The rocks are so young that they appear to fall within the range of error of the radioactivity method of age determination, and fossil evidence is meager. However, it appears that it is possible to assign the ages of at least the main islands to geological epochs, and that is about all that is needed for our purposes. Early in this essay, we noted that the islands are of Tertiary origin. The Tertiary covers an enormous period of time—some 70 million years. A special committee of the National Research Council has recently calculated that the durations of the subdivisions of the Tertiary were about as follows:

Pleistocene	1 million years
Pliocene	11 million years
Miocene	17 million years
Oligocene	11 million years
Eocene	20 million years
Paleocene	10 million years
Total	70 million years

It is obvious that we do not know exactly when these Hawaiian volcanoes first broke out beneath the sea, but we can see, in a broad way, what happened to them after their exposure to the air. It is possible to estimate roughly how much of the islands has been worn off and arrive at an approximate rate of erosion.



It is also possible to ascertain roughly the rates of upbuilding. However, the attempts to date various islands or parts of islands in numbers of years have not been very successful.

Wentworth (1925) studied the island of Lanai in detail and estimated the age as between 131,000 and 200,000 years. His method was as follows: The amounts of outflow of historic lava flows in Hawaii were ascertained and their character fairly well understood; the average volume of Lanai basaltic flows was estimated at 200 million cubic meters; the subaerial volume of the island is equivalent to 580 such flows; on the basis of the frequency of lava flows on Hawaii and elsewhere, and the presence of evidence to indicate that outflow was so regular that no decided erosional intervals were interspaced in the upbuilding period of Lanai, it was estimated that the lava flows "probably succeeded one another at an average interval of not less than ten or more than 100 years." Thus the subaerial upbuilding of Lanai was estimated to have taken from about 6,000 to 60,000 years. (It is worth-while to note here that the historic flows of Mauna Loa during the past century have been estimated at between five and ten billion cubic meters—or enough lava has poured out of that mountain to raise its gigantic dome three to six feet higher in the past one hundred years.) The rate of erosion based upon subaerial removal was estimated at one foot in 2,900 years for Lanai, and the erosional age was thus estimated at 125,000 years. Wentworth concludes that "the first appearance of Lanai above sea level dates from a time well back of the Wisconsin stage of the Pleistocene but not so far back as early Pleistocene if recent estimates of the duration of that subdivision of geologic time are correct. Moreover, if the terrace building epoch indicated by certain features of Oahu be correlated with one of the more pronounced advances of glacial ice in North America, Lanai, which . . . postdates these features, will be at least somewhat younger than early Pleistocene." (1925:55-56.)

It may appear that such a method of age estimation might be applied to all the islands. However, there are many complicating factors that enter into the problem, and such estimates can only be applied to certain restricted areas where a great body of information has been assembled and where the underlying framework is completely understood. It is thought that in some areas of high rainfall the rate of degradation may be as great as a foot in 400 years. Thus most areas in Hawaii are now excluded from such age estimation, for too few data have been collected.

Geologists may be asked what they know about what is hidden beneath the islands, and the good and logical question is advanced, "How do you know that there are not ancient islands buried within the interiors of the present islands which you maintain are young islands?" As a matter of fact, it is known that at least on the islands of Hawaii, Maui and Kauai, and probably on all the islands,

Figure 22.—Kaaui Crater, a youthful volcanic outburst on the rugged, deeply eroded slopes of the Koolau Mountains behind Honolulu. (After Stearns, 1946. Photograph by U.S.A.A.F. Cut loaned by U. S. Geological Survey, Honolulu.)

there are considerably older dissected areas buried beneath the more recent lavas making up the bulk of the islands, and this evidence extends the ages of the islands far back beyond the ages suggested by the much younger surface lavas. The evidence at hand, however, appears to be good enough to enable us to conclude that there are no significant, ancient, unknown islands buried or hidden within or below our mountains. Great canyons like Waimea on Kauai have exposed several thousands of feet of strata which show conclusively what has gone on in past ages of lava flow and erosion. (Newer flows, in which the river is now cutting, have filled part of the bottom of Waimea Canyon to about 800 feet. Nuuanu Valley on Oahu has similar recent flows, as do other valleys.) Also, we have numerous, carefully logged well shafts that have been sunk to as much as 1,500 feet below sea level, and water tunnels have been driven far into, or entirely through, mountains and mountain ranges. Such data are indisputable. These old dissected areas buried by later lavas have been taken into account and are thoroughly considered here.

Wentworth considers that there is no reason to believe that any existing land surfaces in the islands are over 5,000,000 years old, and he said ". . . physical evidence does not appear to indicate the emergence of any part of the Hawaiian group above sea level before the later part of the Tertiary period." (1927:133.) Both Wentworth and Stearns believe that the main islands are Pliocene or more recent and that the bulk of the land of the main islands is largely of Pleistocene age.

Too much assumption and too little actual knowledge are behind much of the reasoning that prompt some authors to voice opinions regarding Pacific island geology. It seems that the only logical course to pursue is that based upon concrete evidence uncovered by the more careful and conservative of geologists who have actually done extensive and critical field work in the islands, rather than to rely upon the imaginative flights of those who conjure up, from fertile imaginations, continents, continental islands, land bridges and ancient islands of great extent for the purpose of solving what appear to be particularly difficult problems of biogeography.

Hereinafter, therefore, this discussion will be based upon the ages of the main islands as is generally agreed upon by geologists. That is, that they are of late Pliocene and Pleistocene age, and the bulk of the erosional and topographical features are largely Pleistocene.

THE COMPARATIVE AGES OF THE ISLANDS OF HAWAII

It has been generally agreed by geologists and biologists that, roughly speaking, there is a progression in age of the islands from west to east—that the older islands are to the west, the younger ones to the east. In the leeward islands are found shoals, reefs, atolls, rocks and volcanic stacks, but the main islands terminate to the east with the young lavas and active volcanoes of the island of Hawaii. Also, in the main islands of Oahu, Molokai and Maui, each of which is formed from the fusion of two major volcanic masses, the western segment

of each appears to be older than the eastern part. However, the picture is not so orderly and simple as it may at first appear. Nothing is known regarding the order of events in the leeward group, but the windward islands present features which lend themselves to at least partial interpretation. Much of what has been said regarding the leeward islands is conjecture—we actually know very little about them. Powers (1917:514) said, "Along the Hawaiian rift the volcanoes have arisen not in exact order from west to east, but in a somewhat irregular manner, with a general migration of the lava in an easterly direction. Furthermore, the order of extinction of volcanic activity has not always been the same as the order of initiation."

Of the various leeward islands, Kaula, Nihoa, Necker, Gardner and French Frigate Shoal have exposures of volcanic rock—the other islands, reefs and shoals are coralline. According to Edmondson (1929), there are no coral reefs on Kaula, Nihoa, Necker or Gardner. The leeward islands appear to be the remnants of high islands, some of which may have been about the size of Molokai, Kauai or Oahu, others larger, while still others were apparently smaller. They appear to be the relics of a decadent mid-Pacific island chain, and there is no reason for otherwise considering them. A knowledge of the island chains of the south Pacific indicates that the usual trend of events in the metamorphosis of such chains has been carried on in Hawaii as elsewhere in the mid-Pacific. Moreover, all evidence shows that this metamorphosis from high islands to rocks, reefs and shoals is vigorously active today, and that it will continue until the main islands assume the general form of the most completely altered of the leeward islands.

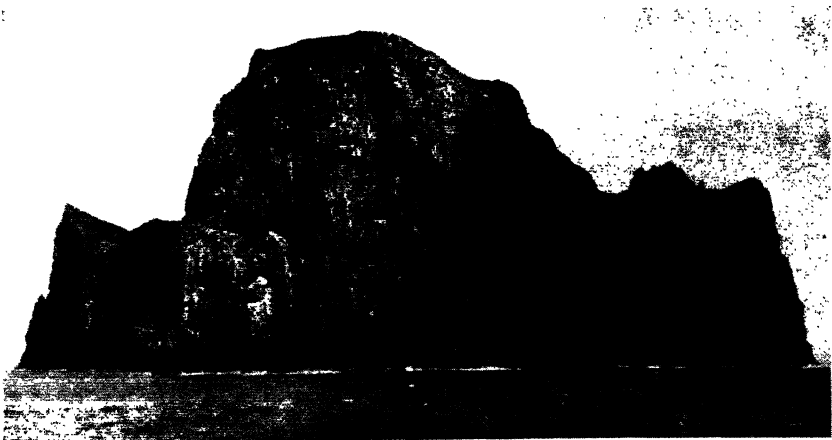


Figure 23.—Nihoa Island, a remnant of an extensively eroded, old Hawaiian island. This craggy mass (895 feet high) of only about 156 acres is all that remains of a former majestic high island many square miles in extent. Note the gentle dip of the lava beds. An extensive shallow bank surrounds the island. (Photograph by E. H. Bryan, Jr.; courtesy of Bishop Museum.)

Palmer has made the most complete survey of the geology of the leeward islands, and he concludes (1927:5) that "It seems logical to believe that the islands and shoals of the northwestern segment were formerly high, volcanic islands much like the present islands of the southeastern segment, but that wave action has completed the truncation begun by wind and running water. The truncated volcanic cones now form submarine platforms, some of which are simple shoals and others are reefs built by marine organisms and enclosing sheltered lagoons above which rise sand islets ten to twenty feet high."

It appears reasonable to conclude that the ancient leeward islands were, at the peaks of their subaerial developments, capable of supporting diversified floras and faunas as typically oceanic in composition as those of the main islands are today. There appears to be no evidence available to use in dating the ancient leeward islands. By way of a guess, and perhaps no one is in a position to do more now, it might be suggested that some of the leeward islands may have been at their zenith in Pliocene or possibly earlier Tertiary time. Obviously, we do not know! Also, I do not now see how it is possible, with our present information, to ascertain the order of emergence, development and degradation of the leeward islands. For the main islands, the problem perhaps is less difficult because we can see the islands in their present subaerial condition. But the task of interpreting their history is not easy. There are a number of complicating factors—geological and biological. As said before (Zimmerman, 1940:273), speaking very broadly and in generalized terms, "The islands are successively



Figure 24.—La Pérouse Rock, vestiges of a decadent leeward Hawaiian island at French Frigate Shoal. Note the flat bedding of the lava flows. The large rock is 122 feet high, the small one 10 feet high. This area is surrounded by a shallow platform 15 miles or more in diameter. (Photograph by E. H. Bryan, Jr.; courtesy of Bishop Museum.)

younger from Kauai on the north to Hawaii with its active volcanoes on the south." However, I do not believe that it has as yet been conclusively shown that Kauai is older than the Waianae Mountains of Oahu, or that part of Molokai is not as old as part of Oahu, or that the Kohala Mountains of Hawaii are not as old or older than West Maui or East Molokai. It appears possible that future evidence may be gathered that would indicate Oahu to be older than Kauai, and Hinds (1931:203) concluded that "The long series of events involved in the development of the Oahu domes and their present landscapes, together with the extent of fluvial and marine removal, lead me to consider both of these domes older than Kauai." Hinds (p. 204) says, "The relative ages of the landscapes of the high old domes appear to be: (1) West Oahu, (2) East Oahu, (3) Kauai, (4) East Molokai; West Maui and Kohala are younger, but their sequence is yet to be determined." Lanai appears to be nearly the same age as West Maui; Kahoolawe may be older than East Maui. Hinds considers the Penguin Bank at the northwest end of Molokai as "...the oldest landscape in windward Hawaii..." and that it "...may be approximately the same age as [that] of the leeward islands." This bank is about 16 by 30 miles in extent and lies under about 25 to 70 fathoms of water. It is doubtful that the data on this bank are complete enough for conclusions to be drawn from them. However, we should keep them in mind in our studies. What appears to be a rather simple problem thus turns out to be a complex one. However, if we keep these facts in mind, I believe that our interpretations of the developments of the biota will be based upon sounder footing than if they are ignored.

PALEONTOLOGICAL EVIDENCE

Fossil insects would probably tell us interesting tales—if there were any fossils! From all the Pacific Basin, I have but one record of an entomological type—that is the finding of a psyllid gall on a fossil leaf of a *Metrosideros* tree in a Recent deposit at Red Hill (near Pearl Harbor, Oahu). To my knowledge, there never has been a fossil insect found on any Hawaiian or other mid-Pacific island. But there is the possibility that someday some may be found. There are certain deposits such as lignite in which some insects might be preserved, but, to my knowledge, no search for insect fossils has yet been made in such materials. Mid-Pacific islands do not provide favorable conditions for the fossilization of insects, and we may expect them to be very rare or absent. On the other hand, fossil land snails and marine fossils are abundant and plant fossils are common in some places. It is significant that no fossils older than Pleistocene have been found in Hawaii; most are Recent.

Marine fossils are found in emerged reefs in many places, and these are most abundant on Oahu. The fossil reefs on Lanai have already been discussed. These marine fossils are of Pleistocene or Recent age. In his paper on fossil marine Mollusca of Oahu, Ostergaard (1928) reports that only three species, two oysters and a *Strombus*, of the 82 fossils studied, appear to be extinct species,

but that the *Strombus* might yet be found living. It is thought by some workers that, if carefully searched for, the oysters may also be found living. Eight species found as fossils in Hawaii are not now known to be living in Hawaii but are found living elsewhere in the Indo-Pacific. Three species are listed as fossils which are also found living in Hawaiian waters but are apparently on the verge of local extinction. About 70 species of marine fossils collected by Stearns at 16 sites on Oahu (Stearns and Vaksvik, 1935:166) and identified by W. C. Mansfield were considered no older than late Pleistocene.

Insofar as is known, all of the fossil plants found thus far appear to be Recent and identical with species now living in Hawaiian forests. A significant point, however, is that present-day upland forest types of plants are found as fossils at low elevations in dry areas where native forest plants have disappeared and where cultivated and immigrant plants now grow.

Fossil land shells all appear to have been found in geologically recent formations. Some of these fossils are identical with living species. Some species have been found first as fossils and later discovered in the living state. Others which are now known only as fossils may yet be found living. However, there is a wealth of Recent fossil species which are evidently truly extinct. In many regions now under cultivation or covered with adventitious vegetation and in dry areas far from the native forests—even on some small, offshore islets—are found rich fossil beds that show without question that these areas were at one time clothed with native plants, as are some of the undisturbed native forests today. Fossil land shells are good indicators of the character of the pre-existing forest cover in a given region, for it can be ascertained from study of them whether the forest was of the wet or dry type. Many of these species appear to have become fossil since man has so drastically upset the balance of native life in the lowlands. Dr. C. M. Cooke, Jr., tells me that there are fossil land shells by the thousands in eolian sand deposits on the island of Molokai. These fossils are so arranged in the sand that it can be ascertained where each tree stood on which the snails lived before they were buried by the drifting sand. Some of the fossil Hawaiian land snails appear to belong to extinct groups of species, but no fossil species has yet been found which belongs to other than a living genus.

Probably the most interesting fossil discovery in Hawaii is that of the bones of a goose taken from an ash a hundred feet below the surface during the excavation of a water tunnel near Kaunaikeohu, Kau, Hawaii, in 1926. Stearns (1930:60) records the following information. "They [the bones] were identified by Dr. A. Wetmore, of the United States National Museum, as those of a peculiar form of goose, representing an undescribed species, distinctly larger than that of the "nene" (*Branta sandwicensis*), the modern Hawaiian goose. The bones lay on top of an ash bed interstratified with basalt and according to W. O. Clark, who forwarded the bones to Dr. Wetmore and who examined the place where the bones were found, the skeleton of the goose was lying on the ash when the lava buried it." This goose has been described by Wetmore, from a few frag-

mentary bones, as *Geochen rhux*, a new genus and species and considered most like an Australian form.

PRE-EXISTING HIGH ISLANDS IN THE MID-PACIFIC

Some authors are persistent in their arguments for mid-Pacific continental land masses or bridges to account for the distribution of Pacific plants and animals. Carl Skottsberg, a distinguished botanist, recently wrote (1940:707) that the composition of the Hawaiian flora "...can be understood only under the supposition that considerable changes have occurred in the distribution of land and sea, *making it possible for plants and animals to travel over land between regions now separated by deep water.*" (The italics are mine.) My own research leads me to take issue with Skottsberg, and I have stated elsewhere (1942:283) that "At least for eastern Oceania the distribution of insects could have been accomplished with little change in the present proportion of land and sea." Such opposite conclusions are characteristic of the literature regarding the distribution of Pacific island life. They are the results of our incomplete knowledge of the history of the Pacific and its products.

Ernst Mayr (1940:200) has the following to say about land bridges in Polynesia:

There was a period early in this century when most zoogeographers were busy manufacturing land bridges whenever they found it convenient to explain certain difficulties of faunal distribution. It is, of course, fascinating to be able to tell the uninitiated: "here are two islands with similarities in their faunas; consequently they must once have been connected! (Isn't science wonderful?)." These efforts culminated, so far as the Polynesian islands are concerned, in the work of F. Sarasin (Nova Caledonia, A. Zoologie, 4:160,1925), who constructed a whole network of land bridges and raised and lowered the sea level by two and three thousand fathoms in quick succession. But even much more conservative authors have always maintained the continental nature of the faunas of New Caledonia, the New Hebrides, Fiji, and other neighboring groups. I, myself, grew up in this belief and was rather surprised when my faunistic studies did not support the contention. They showed, rather, that even the just-mentioned islands are "oceanic."

I believe that those biologists who "create" continental land in the mid-Pacific to enable them to give an interpretation of the distribution of the groups of organisms which they are studying are overlooking the fundamental geologic nature of the mid-Pacific islands. They call for continental land where none is indicated by the geological record. They demand age beyond that indicated by the rocks. They create in their minds the physically and geologically impossible. Our imperfect knowledge of the diverse ways and means of dispersal of plants and animals is not fully recognized even by some of our best students.

An explanation will be offered here to account for the distribution of the mid-Pacific biota based upon what is believed to be foundations in keeping with the geological history of the Pacific Basin, and which at the same time will at least partially reconcile the differences between such opposite points of view as those of Skottsberg and myself. I have said that "Though the evidence for former

extensive land masses is lacking, it is probable that high islands other than those represented on maps existed in past ages.... Such islands, when above water, may have been used by plants and animals as stepping stones." (1942:283.) Herein lies the crux of the situation, I believe.

From a synthesis and analysis of data gleaned from first-hand experience in the Hawaiian, Fijian, Samoan, Society, Tuamotuan, Mangarevan and Austral archipelagos as well as from such scattered islands as the Line Islands, Pitcairn, Rapa and Marotiri, Henderson and others, together with a review of the findings of other workers, the conclusion that many of the islands of the mid-Pacific appear to have passed through or are now passing through a definite cycle of geological metamorphosis that has been essentially similar for most of them is inescapable. This cycle has been outlined in the preceding pages, but it will not be out of place to restate it briefly and simply here. The islands have emerged from the sea, built up by volcanic outflow to various maximum sizes, shapes and elevations; volcanism has ceased; erosional activities have torn at the mountains until the older islands have been washed back into the sea where many of them have been capped with coralline materials and have become atolls, reefs or shoals. There are all stages and intergrades of this metamorphosis plainly visible today. The Tuamotu Archipelago and the Marshall and Gilbert and Ellice and Phoenix islands may be as much a part of this historical process as are the Hawaiian islands. The Samoan, Society, and Austral island chains are extraordinarily similar in basic formation to that of Hawaii as they exist today. According to this view, it is only a matter of time until all of these islands will assume the form of the leeward Hawaiian islands, the "dead" Tuamotus and similar coralline archipelagos.

It is not implied that all of the atolls, reefs and shoals in the mid-Pacific necessarily have the same history. There is no reason why some volcanoes could not

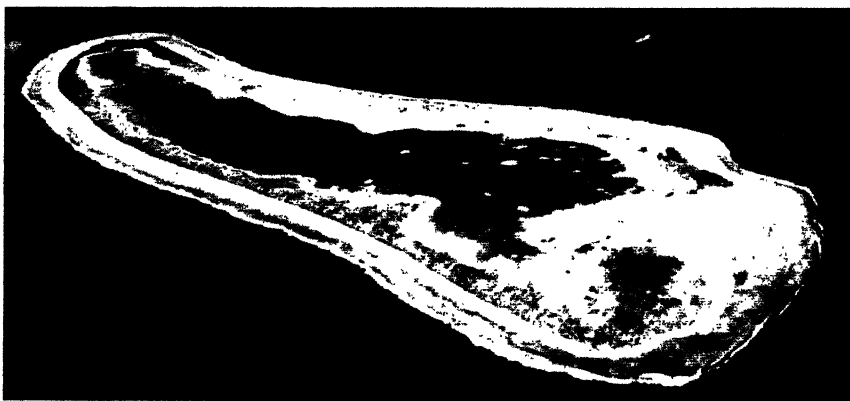


Figure 25.—A small atoll in the Phoenix Islands (Gardner Island).

build up to within the zone of reef-building plant and animal growth and then become inactive. Thus, some of the atolls might conceivably be built upon foundations which have never felt the air. Also, some of the atolls might be built upon volcanic masses that emerged to only a slight elevation above sea level, became extinct and are now capped with coralline growth because of their submergence by the rise of the sea following the retreat of glacial ice. We must also take into account the rise in sea level which has taken place because of the hundreds of cubic miles of water which have been displaced as the result of extensive volcanism, to say nothing of sedimentation and organic deposition. Moreover, there is the possibility of a volcano emerging from the sea, building up for a few hundred feet by erupting ash and cinders, then becoming dormant without capping itself with more resistant flow lava, thus enabling the sea quickly to plane it off below sea level by wave action against the unconsolidated material. Perhaps many atolls have been formed by such a process. We are told by geologists that there has been a submergence in Hawaii of about 1,000 feet; such submergence alone would provide a means of atoll formation from islands up to about 1,000 feet in elevation. In some areas, atoll bases may have been formed largely from the local subsidence of some high islands. But we do not yet know very much regarding atolls and coralline islands in spite of what some workers would like to have us believe! We need some careful work done on typical atolls with adequate borings made in the light of the experience gained at Funafuti and elsewhere (on grid patterns, not random holes). *One of the most pressing needs in contemporary studies of Oceania is deep, core borings on atolls!*

If this line of reasoning be followed, then it may be that during past ages Hawaii was decidedly less isolated than it is now. In other words, I believe that Hawaii is more isolated from other high islands today than ever before. The sea to the south and southwest of Hawaii is now studded with atolls, many of which may mark the graves of large, high islands which at one time were much the same as those of the main Hawaiian Islands or the Society Islands or the Marquesas, or Samoa and others. Perhaps parts of the Marshall, Gilbert, Ellice, Phoenix, Kingman-Christmas chain and Tuamotu islands were at one time or another majestic mountainous islands upon which flourished characteristic floras and faunas. Whereas the nearest high islands today are about 2,000 miles away, in past ages the isolation was possibly only about 500 miles (Johnston Island)—perhaps even less.

Such pre-existing high islands would provide stepping stones for the immigration of floristic and faunistic elements from the Asian, Malaysian, Papuan, Fijian and southeastern Polynesian sectors. It does not call for the jumping over of "thousands of miles" of open sea (as many workers believe is required), but rather for a series of smaller over-water steps.

It appears that not all of these routes were available at the same time. If they existed at different times, the influx of diverse groups of organisms was at different times, at different places, by different routes from different places.

This would account for the apparent differences in age of various sections of the biota. It now appears to me that the route through the Marshall and Gilbert sectors was cut off before that leading from southeastern Polynesia. I would guess that most of the extra-Hawaiian stepping-stone routes were cut off in Pliocene or by early Pleistocene times, that it now appears probable that some sources were blocked off even before the Pliocene, and that the amount of immigration since mid-Pleistocene has been greatly limited. However, there are elements in both the flora and the fauna that indicate that some colonizations have been made since all the high-island stepping-stone routes were obliterated—as they are today. Moreover, there is no reason to believe that natural immigration has ceased or that it was any less rapid 200 years ago than 10,000 years ago. Since the advent of white man, however, conditions have been greatly altered. Various distribution patterns in the Pacific may be the resultants of different stepping-stone access routes being open at different times. Thus, the influx to a given point may have been from different directions at different times.

Normal mid-Pacific atolls cannot serve as favorable stepping stones for high-island floras and faunas, and with few exceptions they support few or no endemic plants or terrestrial animals. The explanation for this is a simple one. The low coral atoll is subject to severe periodic fluctuations of inadequate precipitation; it is exposed to the full fury of storms, those in the hurricane belts are time and again swept bare of soil and vegetation by hurricane-driven waves, and tsunamis ("tidal" waves) may play a definite role. I have seen the results of hurricanes in the Tuamotu Archipelago, and the devastation wrought is a sight to behold. Plants and animals are not normally left undisturbed on an atoll for a long enough time for variation, raiation or speciation to take place. Thus the flora and fauna of the atolls of a great archipelago like the Tuamotu are made up almost entirely of populations of widespread species. Most of the coral islands that do have endemic species are either slightly or distinctly elevated or are outside the hurricane belt. Henderson Island, at the southern end of the Tuamotu Archipelago, is an emerged atoll between 75 and 100 feet high, and it has endemic plants, land snails, insects and even an endemic genus (subgenus?) of birds (a rail)! When an atoll is emerged to an elevation above the point where periodically it can be swept bare of its terrestrial life, it enters into the phase where the development of endemic products is possible. Thus, most of the atolls which have been formed by the degradation of high islands have lost all or nearly all of their original flora and fauna by extermination. They develop the typical atoll association of plants and animals which varies according to the locality and climatic zone, either wet or dry or intermediate. Atolls mostly are ecological deserts unsuitable to most high-island plants and animals, and they cannot act as efficient stepping stones. A sufficient increase in elevation and the subsequent change in environment place atolls in the realm of high islands once again.

CHAPTER 2

DISPERSAL

As the ploughshare breaks up the green sward of arable land, and disturbs the closely interwoven roots of the existing assemblages of plants, so do tornados, whirlwinds, and storms furrow the surface of our globe in all directions, unsettling and scattering prosperous communities of living creatures, and rendering many of them for a time the helplessly drifting waifs of an ocean . . .

—Müller (1871:186)

GENERAL CONSIDERATIONS

A survey of the literature for the past 300 years or so will reveal a multitude of records concerning the many ways and means of occasional transport by which plants and animals are spread about the world. In spite of this great body of information, there are those who still fail to accept the evidence and who refuse to recognize that overseas dispersal to islands is fact and not theory.

Even the most ardent advocate of Pacific continents and land bridges would hardly be so bold as to suggest that each of the hundreds of mid-Pacific islands was at one time connected to some other area by dry land. Some islands have been strictly isolated from the time of their origin and have never known a sub-aerial connection with any other land. But all of the islands that can support a terrestrial biota have been populated by plants and animals. The elementary fact that these islands insulated by ocean barriers have been populated is proof enough that certain plants and animals can cross such barriers of open sea. Therefore, if some mid-Pacific islands have been so populated, then all the mid-Pacific islands including the Hawaiian Archipelago could have been populated by oversea transportation. To argue for land connections is to evade the question. "...if the micro-pulmonates can only travel on land, then well-nigh every island on the face of every ocean is an unsubmerged fragment of some previous continental land-bridge." (Addison Gulick, 1932:416.)

Spitsbergen was entirely covered with ice during the last glacial epoch, and its contemporary terrestrial biota has arrived from overseas since the retreat of the glacial ice has exposed soil. There has been no land connection between Spitsbergen and Europe since glaciation. Elton (1925) found that aphids and flies blow 800 miles from Europe to the islands, and he says that the present insect fauna has arrived principally through the air and on birds.

The uninhabited, isolated, elevated coral atoll, Henderson Island, is again brought to mind. This raised atoll, which is northeast of Pitcairn Island, is about

2.5 by 5 miles in extent and is elevated so that its top is between 75 and 100 feet above the sea. It is, as it exists today, certainly a young island whose subaerial age is to be counted in thousands of years rather than hundreds of thousands of years. The old lagoon depression and its included coral masses and irregularities can still be seen. It appears to have risen sterile from the sea, insofar as its terrestrial biota is concerned, yet it is now densely clothed with a tangled tropical jungle. More than 250 species of plants, mostly native, were found there in 1934 by Bishop Museum's Mangarevan Expedition. There are also endemic birds, including an endemic genus (subgenus?) of rail, endemic insects and endemic land snails. Thus, all of the major elements of the Polynesian terrestrial biota have succeeded in being transported across the sea, colonizing this tiny bit of isolated land, and have not only established themselves there but have evolved into new forms quite distinct from their forebears.

To my knowledge no one has stood on an island and watched hurricane winds blow insects or land snails from another island across the sea, or watched while seeds, insects or land snails were dislodged from birds or from materials drifting in on waves. However, there are those who saw very large sheets of iron roofing torn loose from a church on Tau, Samoa, by a hurricane and others who saw some of that iron crash onto the island of Olosenga six miles away across the sea! The iron could be seen, but not the seeds, small insects and land snails that might have been carried across the channel at the same time. I picked a living bark beetle out of the feathers of an owl knocked down in flight in the highlands of Fiji. Owls have been seen at sea 1,000 miles from the nearest land. Wheeler (1916:180) described a new species of ant from a colony taken from a log which had floated from Brazil to San Sebastian Island. A mallard duck shot in the Sahara had snail eggs on its feet.

These are just a few facts from the body of convincing evidence that shows without a doubt that overseas dispersal is an active reality.

My friend R. H. Van Zwaluwenburg spent about four months on the coral island of Canton (171.5°W 2.5°S) during two successive years and has, fortunately, recorded some of his observations made there. Because of the variation in annual rainfall, the island's vegetation cover ranges from desert-like to lush. During and following a period of dry years when the island was in "desert condition," only an occasional straggling, travel-worn *Hypolimnas bolina* butterfly was seen. After a period of rains which brought up a lush growth of plants from dormant seeds and roots, the butterfly became established from overseas immigrants. Single specimens of the monarch butterfly arrived, but this species had not succeeded in establishing itself up to 1941 (because of lack of a suitable host?). Also, after a period of rainfall which left some persistent ponds, two species of dragonflies became established from immigrant parents. No dragonflies were seen on the island during the previous year. A return to arid conditions would result in the local extermination of the butterfly and the dragonflies.

Van Zwaluwenburg (1942) says, "It seems probable that some or all of the above insects, as well as others similarly capable of traveling long distances,

have been established on Canton at one time or another in the past. The fact that the present establishment of the three discussed is recent suggests that conditions of food and water favorable for their maintenance are only temporary; that establishment and local extinction succeed each other as favorable and unfavorable conditions alternate, and that the present colonies of these particular species will in turn die out when severe drought recurs."

The prevailing winds at Canton are easterly or southeasterly, and the normal current drift is westward. In 1940 few or no seeds were seen among the debris cast up on the beaches. Following a period of strong winds from the west (up to 55 knots), drift-borne seeds were common and conspicuous, and the seeds of about 20 species of plants were picked up. Some of the seeds found were of species which are not known to live on any island closer than several hundreds of miles from Canton.

The insects and seeds recorded here are all large, conspicuous, easily seen objects. How many minute seeds and insects might escape the notice of the observer?

Seeds of many of the species listed had sprouted after stranding. Between 35 and 50 coconut sprouts were estimated to be still present in September along the entire 27-mile perimeter of the island, but these were only a small fraction of the total number of coconuts cast up. Some of the hazards attending the survival of the seedling plants from drift seeds are obvious: hermit crabs (*Coenobita olivieri* Owen) shred the husks of coconuts and eat out the contents of the sprouted nuts; flood tides drench many seedlings with sea water; in at least one case high water buried a sprouted palm deep in sand. So the complete failure of any of the above named plant species to become established on Canton in the past (all of the coconuts growing on the island are known to have been planted by man) is not surprising when, to the hazards already mentioned, are added the inevitable recurrent shortages of rain. (Van Zwaluwenburg, 1942:52.)

The great difficulty in the dispersal of animals from one locality to another on floating vegetation appears to be not so much dependent upon their being cast adrift and being transported, but rather in their landing in another locality and becoming established in a foreign and perhaps hostile environment. Sea beaches upon which flotsam is cast are not usually favorable environments for the establishment of most terrestrial organisms. Many kinds of insects which were purposely introduced and carefully cared for have failed to become established in Hawaii. The number of natural immigrants which have failed to establish themselves after surviving overseas journeys must be very great.

The crux of the problem is that insects, plants and terrestrial Mollusca do inhabit all habitable Pacific islands no matter how great the isolation, and, therefore, they possess advantages that fit them for selection by agents of overseas distribution and for survival. Many of the insect genera inhabiting mid-Pacific islands are flightless descendants of flightless ancestors, and because they inhabit islands separated by hundreds of miles of open sea, their distribution is obviously independent of their ability to walk. Such insects have crossed, and undoubtedly still are crossing, large bodies of open sea, not because they have wanderlust, but because of forces beyond their control—forces undoubtedly adverse to their

general well-being. A bewildering fact is not that these islands have been colonized by overseas dispersal, but that so few animals have crossed the sea and have become established here.

As an example of comparatively recent interisland dispersal, the minute weevil *Microcryptorhynchus vagus* Zimmerman may be mentioned. There are more than 80 species of the genus described from southeastern Polynesia, but all except *M. vagus* are confined to single islands or parts of individual islands. However, *M. vagus* breaks the rule of absolute uni-insular endemism, for I found it on four of the Society islands.

One may be asked, "If such distribution has accounted for the origins of these floras and faunas, why has it stopped? Why do we not find species blowing or drifting in now?" The answer to such questions is simple. What would be the chance of finding a few small seeds, molluscs or insects which might arrive in any one area from overseas? Almost nil, of course. If they became established, one might find a colony before long, but it is too much to expect actually to witness the arrival of such minute immigrants. In another section of this paper I have analyzed the Hawaiian insect fauna and found that over a period of several millions of years, only about 250 overseas stragglers succeeded in becoming established in the several thousand square miles of the Hawaiian Islands—perhaps only one successful colonization per 20,000 years! The very developments of the diverse parts of the biota reflect sporadic and interrupted immigration over long periods of time. Overseas dispersal has not stopped, but we are fortunate when we can record a few concrete facts. Our period of scientific research on such problems is but a passing moment, and we cannot expect to witness everything in a wink of time's eye.

MEANS OF DISPERSAL

There are three principal ways by which the terrestrial endemic biota of the Hawaiian Islands may have reached the archipelago. These are marine drift, wind and aid from other organisms.

The normal, contemporary ocean currents that sweep past the main Hawaiian islands are from the east, but the westernmost islands come within a zone that experiences at least a certain amount of drift from the west. During Pleistocene glaciation, the western current may have shifted farther to the south. Thus the archipelago may have been much more affected by currents from the west in the past than it is now. The problem of past climatic changes is worthy of careful study, and it has not received adequate attention in the Pacific. At the present time, logs from northwest America and fish net floats and other items from Japanese waters are commonly cast upon Hawaiian shores. There appears to be little information available concerning the routes of drift of these objects. It would be most worth while if a study of the material coming ashore at Midway Island, for example, could be made to determine how long the material had been in the water and by what route it had traveled. A study of the marine organisms adhering to floating objects would reveal much pertinent information.

However, the strong, eastward, counter currents set up by cyclonic disturbances should not be overlooked. Probably they are largely to be credited with the spread of the common strand plants that are as a group so similar from Micronesia and Melanesia eastward. Irregular currents may be more successful agents of dispersal than normal currents.

The literature is replete with examples of plants and animals being transported across wide stretches of sea. It is usually only the records of the larger animals that find their way into print, however, and crocodiles, monkeys and large and small reptiles are known to have made their ways, some on identified floating material, across ocean barriers. Wood-Jones (1910:290) records a tree which carried ashore at Cocos-Keeling a wheelbarrow load of soil in its buttressed base, and he considered that a small burrowing snake was carried to the island in such a manner. Large rafts or masses of debris making up "floating islands" are commonly washed out to sea from islands from Fiji westward. It has been shown that such masses may carry with them a varied assortment of plants and animals. Mr. C. E. Pemberton told me that while out of sight of land on a voyage between Macassar, Celebes and Sandakan, Borneo, many "floating islands" were seen. These mats of vegetation were lush and green, and palm trees 20 to 30 feet high stood erect on the floating masses. A survey of these rafts probably would reveal that numerous plants and animals were riding them. Although such rafts are probably broken up by rough water, it is possible that some of them, on rare occasions, could travel more or less intact for many hundreds of miles and deposit at least part of their living cargoes on foreign shores. I have seen large trees washed from stream sides during a storm in Tahiti and have seen them floating out to sea with their large branches riding high out of the water. The large, heavy trunks, great root masses in which are entangled stones and soil, and the submerged limbs may act as keel, ballast and stabilizers and hold a part of such floating trees permanently out of the water. Some of the branches may be held 20 or more feet above the waves. At rare intervals, colonies of animals and seeds may be able to survive lengthy journeys in such perches. It is conceivable that over a period of several millions of years a few such floating trees have been beached in Hawaii and that from them there escaped ancestors of some of our insects, terrestrial molluscs and plants.

Visher (1925:122) said:

The floods caused by the excessive rainfall associated with hurricanes influence the dispersal of land forms. There are numerous records of the fall of more than twenty inches in two days, and some records of more than sixty inches in three days. Under such conditions streams normally small may become great rivers and carry to sea vast quantities of driftwood. The river banks are eroded badly, and many trees are undercut and are carried out to sea. During the excessive rains, large masses of dirt and loose rock upon steep hillsides may slip, sometimes damming valleys. If the dam breaks, the sudden rush of water does its part to contribute natural rafts of driftwood with their load of land animals and seeds. Hence, the absence of long rivers flowing to the Pacific, with the exception of the Chinese rivers, should not lead to the assumption that natural rafts of considerable size and biological dispersing possibilities are lacking in the Pacific. Pilsbry has made this erroneous assumption. He states: "The argument

of the distribution of animals by natural rafts has never been more convincingly stated than by W. D. Matthew in his paper 'Climate and Evolution.' Much of his argument is not applicable to the Pacific islands. Here we have no large rivers to give forth natural rafts. If a single tree washed to sea it must be very exceptional."

Perkins (1913:lxvi), speaking of the dispersal of Hawaiian land snails, said, "We once found at the foot of the Waianae slopes a number of one of the terrestrial species of *Amastra*, quite outside of the forest, hiding in the hollows of a large log on the bank of a stream. This log had clearly been carried down in a flood, and probably for many miles before stranding, the stream arising in the Koolau range of mountains, the forest of which was miles distant."

However, because of the concomitant difficulties in transportation and establishment, it appears that marine drift is probably the least successful of the three methods of transport.

The bulk of the insect faunas of the mid-Pacific appear to me to be wind-borne. Adequate experiments have now been carried out to show that both winged and wingless insects are carried by air currents to great heights: The work of Glick (1939) has been previously reviewed and the interested reader is referred to his extensive discussion of the records obtained during a five-year period of trapping insects in the air by the use of airplanes. "Not only were thousands of insects taken at various altitudes up to 14,000 feet, but spiders and mites, wingless creatures, were not uncommonly captured. One spider was taken at 15,000 feet. Some opponents of dispersal by wind say that certain insects are weak fliers and are therefore not capable of traveling great distances on the wind. These weak fliers are just the insects which Glick found to be the most abundant in the air and which were carried to the greatest heights. Heavy-bodied, strong-flying insects were not taken high in the air. Not only were winged adult insects collected, but larvae, nymphs and wingless adult insects were captured as high as 14,000 feet. Glick says that these wingless forms are all at the complete mercy of the upper air currents." (Zimmerman, 1942:287.) An analysis of the endemic Hawaiian spider fauna shows that it is made up only of those groups that can be wind-borne; all other groups are absent.

It is not considered that normal trade winds are strong enough to blow even small insects for significant distances across open bodies of sea. The trade winds of the Hawaiian area blow from the east. In another section it is shown that relatively few insects have been derived from America. Therefore, the normal trade winds cannot be considered as primary agents for the dispersal of the predecessors of the Hawaiian insects. Also, the unbroken distance between America and Hawaii is great. However, it is largely abnormal rather than normal conditions that have accounted for the dispersal of the mid-Pacific biota. In reviewing the distribution of south Pacific insects (Zimmerman, 1942), it was noted that hurricanes have often swept from the west, crashed through insular forests stripping trees of their leaves and twigs, churned across the sea and passed over islands eastwardly of their origins. It is such abnormal, cyclonic winds which I believe have accounted for the dispersal of a large part of the

insects of the mid-Pacific. Convection currents may carry insects high into the air to the anti-trade wind zone which blows strongly from the west, and upon attaining these high strata, insects might be transported for considerable distances.

The force of hurricanes is probably underestimated by those who have not actually experienced them or seen what they can do. "Men instinctively underestimate the lifting power of air. Many zoologists today find it as difficult to believe that winds and rising air currents can lift and carry moderately heavy organisms as persons once found it to believe that heavier-than-air machines could fly." (Darlington, 1938:280.) A wind of 75 miles per hour is said to have a force of more than 16 pounds per square foot. Cyclonic winds with speeds in excess of 150 miles per hour have been recorded on Pacific islands. The pressure of the wind increases as the square of its velocity. The force of such winds and the devastation wrought are astounding. Great blocks of coral reef as much as 30 feet high may be ripped up by the wind-driven waves and brought to rest on shore. Stone buildings are blown down, and the amount of plant material thrown into the air is great. Leaves and twigs hurled high into the air may well act as conveyances for flightless creatures which cling tightly to such material or which are living within it. It hardly seems necessary to point out the great increase in buoyant capacity with decrease in size of organisms. Thus, air currents which cause little concern to a man have a drastic effect upon small organisms whose surface is so greatly increased in proportion to their weight. Visser (1925: 120) said:

Is it not highly probable that tropical cyclones have played a part in the dispersal of life from island to island in the Pacific? Along the Equator are many violent westerly winds, completely overcoming the prevailing easterlies; within the Tropics or just beyond the Tropics many storms move eastward. In moving eastward, the strong westerly wind on its equatorward side carries much with it, and sets up a strong drift as well.... The power of the wind to transport light objects through the air, as for example when birds and insects are carried out to sea in large numbers, is illustrated by hurricanes. Indeed the presence of butterflies and birds far out at sea has often been noted in connection with hurricanes.

On page 124 he says:

It is conceded that the effects of a single hurricane are small, and the reason why hurricanes have been largely ignored by the students of plant and animal distribution is because hurricanes were believed to occur only at long intervals. But now that the records show more than two score annually, on the average, in the Pacific, hurricanes take on a different aspect and their significance is increased by the fuller appreciation of the diverse ways in which they affect the lands, streams and currents.

On occasion, sand from the Sahara Desert is blown as much as 400 miles to sea where ships have experienced sandstorms and have been littered with sand.

Notations are made of the birds, butterflies and large insects which can be readily seen, but the minute insects which cannot be seen except when close to the observer usually escape the records. Butterflies, dragonflies, Orthoptera, beetles, bugs, flies and other insects have been recorded at great distances from shore. Some insects have been taken at sea as much as 1,000 miles from their

homes. Land snails from Cuba have been carried to Florida by hurricanes, and numerous colonies are now established on the mainland. A Pan-American Airways employee told me that after a westerly storm of several days' duration, a Chinese cuckoo came ashore at Wake Island. A pair of North American kingfishers flew ashore on the island of Hawaii a few years ago. *Proterhinus* (flightless) weevils were found by Perkins to have been blown far from their food plants, and he found (1913:lxvi) land snails which had been carried by the wind on leaves or small branches to a barren, treeless area on Molokai during a severe gale. Hardy and Milne (1937) flew kites carrying traps and attached nets to the masts of ships and found that the amount of "aerial plankton" drifting across the North Sea was considerable. They caught spiders, Hemiptera, Neuroptera, Trichoptera, Lepidoptera, Hymenoptera and Diptera at sea. "After reading about the recent developments of our knowledge of the upper air-strata, I am inclined more and more to regard the trans-oceanic distribution of insects as carried out mainly in the upper air." (Guppy, 1925:543.)

Overseas dispersal aided by birds is probably next in importance to occasional transport by wind, and in certain instances it may be more important. It appears that the role played by birds in the dispersal of the terrestrial floras and faunas of Pacific islands is underestimated. Numbers of sea birds such as shearwaters, terns and tropic birds nest in insular forests from sea level to over 6,000 feet. Some of these birds burrow in the soil or nest upon the ground in the midst of dense plant growth, while others build their nests in shrubs and trees. I have observed white-tailed tropic birds nesting in the high interior rain forests of Samoa. These birds build their nests in *Asplenium nidus* ("bird nest") ferns and on epiphyte-covered branches of trees. When they alight, they claw at and beat the surrounding foliage with their wings. By these clumsy actions they dislodge insects, land snails and parts of plants. The habits of such wide-ranging birds fit them admirably for having insects, land molluscs and seeds lodge on their bodies and thus be carried for long distances to other localities. Cyclonic winds will drive such birds out of their mountain haunts and they may not alight until another island many miles distant is reached. There are those who may belittle the importance of this possible means of dispersal, but we need only recall the record given previously of the finding of a living bark beetle on an owl (an owl was captured after it alighted on the "Duchess of Richmond," a thousand miles at sea in the Atlantic in 1938), that Perkins found a living achatinellid land snail on a Hawaiian bird, that a mallard duck shot in the Sahara had snail eggs on its feet and that experiments have shown that seeds are carried for long distances by many kinds of birds, to have the possibilities of dispersal aided by birds forcefully illustrated. No survey has been made of the foreign material adhering to birds in the Pacific. We do not know how much plant and animal life is carried by birds across the sea. It is highly probable that the several kinds of Boreal plants found on Hawaiian mountains, as well as certain land snails which are identical with, or closely similar to, certain northwestern American species, have been accidentally brought to Hawaii by birds. Ducks, geese,

plover, sandpipers and about 40 other kinds of birds stray or regularly migrate to or through Hawaii from northwestern America. Some of these birds continue on to islands in the south seas, and pass back through Hawaii on their return to northern latitudes. In 1943 a flock of ducks landed at Palmyra Island, about a thousand miles south of Honolulu. Some of the ducks bore tags which had been placed on them in Utah. It is much more unlikely, however, that organisms coming from the north would become established here in Hawaii than would those from the south or west, because of the dissimilarity of the environments between high latitudes and tropical Hawaii. The comparative paucity of Boreal elements in the Hawaiian biota is easily understood, and the few exceptions only emphasize the general conclusion as to the tropical derivation of the biota. It may not be out of place to note here that a cuckoo migrates regularly over an east and west route in the south Pacific. I have seen the species as far east as Mangareva.

Some malacologists are reluctant to admit that land snails can be transported across ocean barriers. It has been said that the large snails such as the Hawaiian achatinellids and amastrids are particularly unsuited for such distribution. However, if we approach the problem differently, different conclusions may be reached. If, as I believe, the large Hawaiian snails have evolved from small or minute ancestors, then the argument based upon their large size loses its weight. However, if small snails can be distributed overseas, then what is to prevent eggs or tiny, immature specimens of large species from being similarly transported?

I agree with Mayr when he says (1940:201):

The means of dispersal of most plants and animals are much more extensive than was formerly realized, and even rather irregular distributions can be explained without the help of land bridges. Dispersal across the sea is, of course, most obvious for birds, and ornithologists were among the first who accepted the ideas of the permanency of continents and oceans. Most entomologists are also beginning to realize that they can solve most of their distributional difficulties without land bridges. The conchologist, however, postulates even today continental connections between all or nearly all the islands where land shells exist. It seems to me that the wide acceptance of land bridges by conchologists is chiefly due to three reasons: (1) our almost complete ignorance of the means of dispersal of snails, (2) our lack of knowledge of the speed of speciation in snails, and (3) faulty classification, particularly generic classification. A. Gulick has already directed attention to the presence of snails on most oceanic islands. They were unquestionably carried there by some unknown means of transportation. Occasionally we must accept this even for larger snails. If one (or several) species of the large snail *Placostylus* are found in northern New Zealand, I would not, as Hedley did, create a continent embracing all the areas where the genus *Placostylus* is found (New Zealand, New Caledonia, New Hebrides, Solomon Islands, and eastern New Guinea), because the acceptance of such a land mass is contrary to all the other evidence. To me it seems incomparably simpler to assume a still unknown method of transportation than a land bridge that is unsupported by any other fact.

H. B. Baker, who has published the most modern monograph on Polynesian snails, states (1941:350) that "The most probable method, by which the accidental introduction of these land snails might be accomplished, would appear to be their rare transport by birds. As is known, certain of the latter, such as the golden plover, do annually migrate through Hawaii to islands in the south central Pacific

and might occasionally transfer eggs, juveniles, or even adults." Baker (1941:355) also states that the long axis of the distribution of the Philonesiae snails from Hawaii to Rapa, which corresponds with the distribution of the recent Nearctic groups which have colonized Hawaii and Tahiti, "suggests that bird transport may also have been a factor in the dissemination of these Microcystinae."

The transportation of snails by birds has not been well understood. There is a genus called *Succinea*, found not only on our islands, but also on many remote islands out in the ocean. *Succinea* has been found on the plumage of birds, and it can hardly be doubted that it thus reached various oceanic islands, but at very rare intervals. There is a remarkable genus of slugs called *Binneya*, discovered on the small Santa Barbara Island long years ago. Last year I found a couple of *Binneya* shells in a superficial deposit on San Nicolas Island. Far to the south, *Binneya* is also found on Guadalupe Island, but, as Pilsbry has shown, the species is distinct. It is difficult to understand how such an animal could cross the sea, but it is known that in the dry season it is covered with a mass of dried mucus which protects it from desiccation. It can be supposed that this sticky mucus, when fresh, might cause the slug to adhere to some bird, and thus obtain transportation. It is not surprising that actual proof of such transportation is rarely to be had; the event must be a very rare one, as otherwise the insular races, evolving under conditions of isolation, would be swamped by newcomers. (Cockrell, 1939:103.)

It should be emphasized here that conditions in the Hawaiian Islands have been changed drastically since the introduction of man, dogs, cats, swine, rats and the mongoose. The sea birds at one time nested on the main islands in myriads, as they do on certain other islands today. The sea birds no longer can use the main islands as they once did. Furthermore, these birds have had their numbers reduced to a small fraction of what they once were. We are apt to overlook these great changes which occurred before we began our studies. The change which has taken place in the development of the sea birds in Hawaii has been a profound one.

One of the most conspicuous features of the insect faunas of the eastern oceanic islands is the entire absence of some large groups, families and orders common to all continents. They have been eliminated by the selective agents of overseas dispersal. Scarab beetles are one of the most dominant groups of all the continents, yet there is not a single native species on the central Pacific islands east of Fiji. Most of them are subterranean in their larval stages, and most are strong fliers. The family is greatly developed in western Oceania. To my knowledge, the only native beetles with true subterranean larvae that occur on the islands of Oceania east of Samoa belong to the flightless genus *Rhyncogonus*—but the eggs of these weevils are deposited on leaves. The absence of endemic Chrysomelidae, or leaf beetles, from Oceania east of Samoa is difficult to explain; they are extensively developed in the western Pacific. With few exceptions, the entire endemic beetle fauna of southeastern Polynesia is composed of small, predominantly flightless species which breed in dead twigs, dead leaves or in or under dead bark, and these forms are more extensively developed than any of the other groups of terrestrial animals in that region.

We will do well to keep in mind Darwin's remark, "How ignorant we are with respect to the many curious means of occasional transport."

CHAPTER 3

ANALYSES AND SUMMARIES OF THE HAWAIIAN BIOTA

A classification which shall represent the process of ancestral evolution is, in fact, the end which the labors of the philosophical taxonomist must keep in mind.

—Huxley

The total number of insects recorded from the Hawaiian Islands exceeds 5,000 species, but many other species are known that await determination or description, and untold numbers of new species have yet to be collected from their mountain haunts. This assemblage is composed of two distinct elements—one native, the other foreign. Only the native insects will be included in this analysis, because it is limited to a discussion of the fauna of Hawaii before the advent of man so greatly disturbed the environment.

ENDEMIC AND INDIGENOUS, IMMIGRANT AND INTRODUCED

It is worth while, before proceeding, to define certain terms as they are used in this text to obviate the possibility of misunderstanding. In using the word *native*, reference is made to those insects which are either *indigenous* or *endemic*. *Indigenous* species are those which live naturally in Hawaii as well as in some other place or places, and whose distribution came about without the intervention of man. As an illustration we may use the ectoparasitic louse fly, *Olfersia spinifera* (Leach) (Hippoboscidae). This fly is a parasite on such sea birds as the frigate bird, which ranges far and wide among Pacific islands. These birds are found naturally in Hawaii, but also on many other islands. The fly has followed its hosts for untold thousands of years, and it is thus *indigenous* to Hawaii, but not *endemic* to Hawaii alone. Species *endemic* to Hawaii are those which are entirely restricted to Hawaii and are not naturally found elsewhere. As an example of an *endemic* insect we can list the ground beetle *Blackburnia insignis* Sharp (Carabidae) which has been found only in a restricted area in the Kaala section of the Waianae Mountains of Oahu and nowhere else in the world. Moreover, the genus to which it belongs is endemic, for it is found only on Oahu.

The foreign insects may also be placed in two categories. The first of these are the *immigrant* species, or those which have been unintentionally brought in by the intervention of man. Such insects are the granary weevils, which have come in cargos of rice, flour or other such materials, or the dozens of species of scale insects which rode into Hawaii on plants brought here for planting or

on imported fruits and vegetables. The majority of our more than 1,300 foreign insects are immigrants. The second group of foreign insects are the *purposely introduced* species. The many species of parasitic or predaceous insects purposely introduced to aid in the biological control of insects and plants come under this heading. We are likely to use the term *introduced* loosely and to apply it to any foreign insect—I have unintentionally done so myself. But, according to some entomologists, it appears that, strictly speaking, the word *introduced* should be reserved for those species which have been purposely imported and not applied to accidental immigrants. However, I can see now no good reason why the qualified phrases *natural immigrant*, *purposely introduced* and *accidentally introduced* are not equally acceptable.

It is not always easy to tell to which of these four categories a particular species belongs. Fortunately, records of importation have been kept for most of the purposely introduced species. The common immigrant household pests such as cockroaches are also easily placed. Some species which we know are immigrants have been described from specimens collected in Hawaii and, because of our incomplete knowledge of other regions, these species have not yet been found in their native lands, and we do not know whence they came. Some species are considered as probably indigenous, but are not yet known from any other locality. However, some indigenous species known only from Hawaii when first described have since been found living natively elsewhere. The majority of the endemic species have definite characteristics which stamp them as endemic, and some of these features will be outlined in the following section.

THE INDICES OF ENDEMICITY

The natural evolutionary products of Hawaii for the most part have dominant characteristics of endemism. A number of rules can be formulated to distinguish them, but, as with so many other natural phenomena, there are numerous exceptions to most of these rules. Some of the significant characters of endemic insects are as follows:

1. Most endemic species belong to Hawaiian species complexes. In other words, an endemic species usually is one that belongs to an association of Hawaiian species which are closely allied to one another or show obvious genetic community of origin. As examples of species complexes we may take extremes such as the genus of small moths, *Hypsmocoma*, with more than 200 described Hawaiian species, or the genus of small, flightless beetles, *Proterhinus*, with its 181 described Hawaiian forms. On the other hand, the singular, flightless stag beetle, *Apterocyclus honoluluensis* Waterhouse, is an endemic species belonging to a monotypic endemic genus. It is a polymorphic species, but evidently none but the single species restricted to the high mountains of the island of Kauai exists. This stag beetle, it is true, does not belong to a species complex, but it is distinctly isolated from any species known from the rest of the world. It appears to be a

relict form. The cosmopolitan butterfly genus *Vanessa* is represented in Hawaii by a single endemic species. This butterfly, as an adult, is not greatly different but yet is unlike any other member of the genus, but, according to Perkins, its larva is so distinct from other *Vanessa* larvae as to make it appear almost to belong to a different genus. It may be that compared to the *Hyposmocoma* and other lepidopterous complexes this single species of *Vanessa* is a newcomer to Hawaii. But its habits and make-up may be such that it would remain as a relatively stable species for a long period of time within the islands, yet develop certain unique characteristics as a Hawaiian species. It appears most probable that it has been derived from a comparatively recent (geologically speaking) natural immigrant, but it cannot now conclusively be shown that this is true.

Perkins had similar views in mind when he wrote (1913:cx1v),

Many of the endemic genera, that contain a single, or a few species, are clearly offshoots from other of the larger endemic genera, or as one might say, they are species of these genera, which have diverged more widely in structure than the average. . . . While therefore the apodemic genera are usually very distinct or remote from one another, the endemic are often closely allied to one another, in such a way as to form aggregates of several allied genera, these aggregates being generally remote from one another and more nearly corresponding to the apodemic genera than do the individual genera composing them.

2. Most endemic insects are confined to native forest plants. Many of them are highly specialized in their host specificity. Some species are confined to a group of allied plant genera, others to a group of allied plant species, others to a single plant species, and others appear to be so specialized as to breed only on a particular variety of a plant species. Many species which are not herbivorous are also confined to certain species of plants. Some groups of Hawaiian insects are so host-specific that it is at times possible to determine a species by being given only its genus, the locality at which it was found and its hostplant. However, there are some exceptions to this rule. In *Nysius*, a genus of true bugs, certain endemic species may be found in great numbers on introduced or immigrant plants such as foreign *Portulaca* and amaranth. In fact, at least one of these species has the appearance of an immigrant, although it is a true endemic insect. If it were a plant it could well be called a "native weed." It is one of the few endemic insects that has been able to break out of its native realm and take to foreign plants outside the primitive forests.

3. Most endemic insects are confined to the mountain forests and are now reduced in numbers or are exterminated in the lowlands because of deforestation and pressure of immigrant enemies. Most of the endemic insects have been exterminated throughout the range of the voracious immigrant ant *Pheidole megacephala*, which is widespread from sea level to about 1,500 to 2,000 feet, more or less, according to locality and rainfall. However, some endemic insects, especially certain Heteroptera and Homoptera, have not been killed off by the ants and are even now widespread and thriving in the lowlands. Also, some species have quickly taken to immigrant or introduced lowland plants, especially, when the foreign plants belong to the same or allied genera as their native hosts.

4. The majority of endemic species have a restricted geographical range. Most of the endemic species are found on single islands; many of them are restricted to certain mountain ranges, individual mountains or valleys or restricted ecological zones within single islands. However, some endemic species are found on most or all of the six main high islands, and some are found on two or three adjacent islands. The family Carabidae, or ground beetles, presents a good example of restricted specific distribution. Of the 222 certainly endemic species, only five are found on more than one island. Thus, almost 98 percent of the Hawaiian Carabidae are confined to single islands. Additional analysis would show that the species are further restricted to definite ranges within particular islands.

As an uncomplicated example to illustrate the foregoing discussion of endemism, let us examine the beetle family Anobiidae. There are two groups of species—one foreign, the other native. There are three foreign species, each of these species is in a different genus, and each genus is in a different tribe. All three species are widespread immigrant pests of considerable economic importance to stored produce and other materials both in Hawaii and elsewhere. The native group includes 140 species and 19 "varieties" (some of these so-called varieties may be subspecies or species), and these 159 forms belong to three genera—an average of 53 forms per genus, all of which are endemic. The three genera belong to two tribes; two of the genera are endemic, and these belong to the same tribe. Almost all of the endemic species are now confined to the native mountain forests, and with the rare occasional overlap of hostplants on the part of a very few species, all are attached to native plants. About 80 percent of the species are confined to single islands, and some of these are further restricted to particular areas within single islands.

THE PERCENTAGE OF ENDEMISM

The usual figures of endemism are misleading. Authors tend to take the total number of species present in an area as a base and derive a percentage from that number. However, the proper procedure appears to be one based upon the native insects alone and excludes those brought in by the interference of man. Imported parasites and accidental immigrants brought in on plants, agricultural produce and other materials from diverse parts of the world should not be considered in the same light as those derived by natural means over millions of years. Should an island on which there are found species of endemic bats be considered to have less than 100 percent native mammalian endemism because man has recently invaded the area and brought in horses, cows, sheep, goats, pigs, rats, mice, dogs and cats? Of course not. By the usual method of citing percentages of endemism, each year would find a decrease in the percentage of native species because of the continual immigration and importation of foreign species. On this basis, then, the number of *native* Hawaiian insects is taken as 100 percent. The number of *indigenous* species has been found to be surprisingly small. The percentage of endemism among the native Hawaiian insects approximates 99 percent!

THE ORDERS OF INSECTS IN THE ENDEMIC FAUNA

The number of orders of insects in the world has not yet been definitely agreed upon by entomologists. In the 1933 edition of Comstock's *An Introduction to Entomology* there are 25 orders listed; Imms, in his 1934 edition of *A General Textbook of Entomology*, lists 23 orders, but Essig, in his recent *College Entomology* (1942), lists 33 orders. Essig's high number is reached by dividing the Thysanura into Thysanura and Aptera, by separating Grylloblattodea, Blattaria, Phasmida and Mantodea from the Orthoptera, splitting off the Diploglossata from the Dermaptera, the Zoraptera from the Corrodentia, separating Anoplura and Mallophaga and removing the Megaloptera and Raphidiodea from the Neuroptera. There appears good reason to divide some of the orders, but it does not seem that undue splitting of other orders is necessary. For example, should the obviously allied grasshoppers, cockroaches, mantids and phasmids each be given a high rank equivalent to that of such distinct groups as the beetles, wasps and flies at the other end of the series? It appears that a more logical system would place the five main divisions of the Orthoptera as suborders. However, this is not the place to enter into a critical discussion of such problems. For comparative purposes, I believe that the most recent list, but the least conservative one, of 33 orders will place the greatest emphasis on certain features which I wish to bring out in this book. Therefore, I shall adopt Essig's list of orders for this analysis of the Hawaiian Insecta.

The listing of the orders in which there are native representatives in the Hawaiian fauna is not so easy as it might appear. For example, there have been 32 species of Collembola recorded from Hawaii, but it cannot yet be shown that any of the species are native insects. Our knowledge of the order from the world as a whole is too poor to enable a conclusion to be reached. On the other hand, there are some species which might be native. As a whole, however, the Collembola appear to be immigrant insects, and for the purpose of this study, I shall place these dubious groups on the non-endemic list.

The orders of insects which appear to have native species in Hawaii are as follows:

- | | |
|-----------------|-----------------|
| 1. Thysanura | 7. Hemiptera |
| 2. Orthoptera | 8. Neuroptera |
| 3. Corrodentia | 9. Lepidoptera |
| 4. Mallophaga | 10. Coleoptera |
| 5. Odonata | 11. Hymenoptera |
| 6. Thysanoptera | 12. Diptera |

THE ORDERS OF INSECTS UNREPRESENTED IN
THE ENDEMIC FAUNA

There are 21 (63 percent) of the orders of insects unrepresented in the native fauna. Fifteen of these 21 orders are now represented in the islands by immigrant species, and the only orders not yet established are Grylloblattodea, Diploglossata, Plecoptera, Megaloptera, Raphidiodea and Mecoptera. It will be worth while to review the 21 orders of insects not found natively in Hawaii.

1. Protura. These peculiar, minute, soil- and humus-inhabiting organisms have been known only since 1907. Since that time species have been described from widely separated places about the world. Specimens have been found in the soil of sugarcane and other fields on Oahu, but these specimens were never identified. There appears good reason for believing the material to represent an immigrant species, however.
2. Diplura. There are four species belonging to four genera, two in the Campodeidae and two in the Japygidae recorded from Hawaii. One (*Japyx*) has evidently not been found elsewhere, and, although I am listing it as adventive, it may some day be found to be native. The Diplura are blind inhabitants of soil, humus and rotting logs and are comparatively poorly known, although they are world-wide in distribution.
3. Collembola. Collembolans make up a considerable part of the insect faunas of most continental regions, but they are a poorly known groups of organisms. There have been 32 species belonging to 24 genera included in the families Hypogastruridae, Onychiuridae, Isotomidae, Entomobryidae and Sminthuridae recorded from Hawaii. Of these, all but five species appear to be, without question, immigrants. The remaining five may also be immigrant species, and I am not including any of them as probable natives for this reason. None of them has all the characteristics of the endemic insects.
4. Grylloblattodea. Only a few of these wingless cricket-like insects are known, and these are restricted to certain snowy mountain areas in western North America and in Japan.
5. Blattaria. There are 18 immigrant cockroaches included in 15 genera in Hawaii. Although some other Pacific islands have native species, all the Hawaiian species are adventitious. Australia has a particularly rich and diversified cockroach fauna.
6. Phasmida. There are many native species of leaf and stick insects in the southwestern Pacific, but none has reached Hawaii.
7. Mantodea. Mantids are common in Australia, New Guinea and adjacent islands, but the only species we have in Hawaii are three immigrants. One is a native of Australia, one is recorded from Java, China and Japan, and the other is recorded from Java and the Philippines.
8. Dermaptera. There have been 12 earwigs belonging to 8 genera recorded from Hawaii. Most of these species are widespread insects, but a few have been described from Hawaii. However, there appears to be more reason for believing all the species to be adventive than to consider that any of them is a native insect.
9. Diploglossata. Only two species have been discovered in this order. Both of these insects are ectoparasitic on rats in Africa.
10. Plecoptera. Stoneflies (which are thought to be among the most primitive of living winged insects) are not represented on any Pacific oceanic islands. Their larvae are aquatic.

11. Isoptera. Although the south Pacific islands from Samoa and Fiji westward are richly endowed with native termites, no endemic species exists in Hawaii. Four immigrant species belonging to four genera have thus far become established in Hawaii.
12. Embioptera. A single immigrant species that is found widespread throughout many Pacific islands now also lives in Hawaii.
13. Zoraptera. One probably immigrant species represents this small but widespread order in Hawaii.
14. Anoplura. No native sucking lice are known in Hawaii. The lack of native land mammals (excluding bats) accounts for their absence. A few common immigrant species are now found on immigrant and introduced mammals.
15. Ephemeroptera. The may flies, whose larvae are aquatic, did not reach Hawaii naturally. The nearest islands in which members of this order have been found are the Samoan group where there is a single native species known. A foreign species has recently become established here, however.
16. Megaloptera. The sialids or dobson flies also have aquatic larvae. There are a number of species found in Australia and New Zealand (and also on the continents), but to my knowledge none has been found on oceanic islands.
17. Raphidioidea. This group is represented only in America and Eurasia with about 95 percent of the species confined to the Holarctic region. None is known from the Pacific.
18. Mecoptera. The scorpion flies are thought to be the oldest insects yet found in the fossil state (lower Permian) that belong to groups having complex metamorphosis. Most of them have terrestrial larvae. The order is world-wide in distribution with the greatest concentration of species in Asia and the Indo-Australian regions. None has been found on any mid-Pacific island.
19. Trichoptera. No caddice flies are native to Hawaii, but I recently found an immigrant species about some lily ponds in a Honolulu garden. Caddice flies are found natively in Samoa and are abundant from Fiji westward. Their larvae are aquatic.
20. Strepsiptera. Although a species and a variety of *Elenchus* have been described from Hawaii, in addition to a known immigrant species, I am inclined to consider all of the forms adventive. Little is known regarding these insect parasites in the Pacific, and only a few species have been discovered on islands.
21. Siphonaptera. There are seven kinds of fleas known in Hawaii, and all of them are adventive. One species was described as *Xenopsylla hawaiiensis* Jordan from an immigrant rat (the "native" Hawaiian rat presumably entered Hawaii by the canoe transport of the early Hawaiian immigrants, and I do not class it as endemic). *Xenopsylla hawaiiensis* now is considered to be a synonym of a southwestern Pacific species.

Thus, the 21 insect orders which are not represented in the endemic Hawaiian fauna may be placed in the following categories:

1. Four orders having exclusively aquatic larvae: Plecoptera, Ephemeroptera, Megaloptera, Trichoptera.

2. Three orders containing apterous, mostly delicate, minute, many blind, moisture-loving dwellers of damp soil or damp humus: Protura, Collembola, Diplura.

3. Three orders of external parasites principally restricted to mammals: Diploglossata, Anoplura, Siphonaptera.

4. One order of rather obscure insect parasites: Strepsiptera.

5. One order of aberrant orthopteroid insects containing a few species restricted to certain high mountain snow-field country in western North America and Japan: Grylloblattodea.

6. One order of terrestrial insects almost entirely confined to the Holarctic region and with no representatives in the Australia-Pacific area: Rhaphidioidea.

7. One widespread order of specialized forms, whose females are wingless; found under bark, under stones, in trash and humus: Embioptera; and one specialized, small order containing only about 20 known, delicate species which live in rotting wood: Zoraptera.

8. One small, ancient order of mostly terrestrial predaceous insects: Mecoptera.

9. One widespread order of specialized wood eaters: Isoptera.

10. Four orders of mostly ancient, widespread, apparently easily adapted, mostly orthopteroid insects: Blattaria, Phasmida, Mantodea, Dermaptera.

It will be noted that most of the ancient orders of insects are not represented by endemic species in Hawaii, and those that are present are poorly developed. The orders most extensively developed in the islands are geologically the youngest. None of the aquatic orders is present with the exception of the hardy, strong-flying Odonata, in spite of the favorable, abundantly watered environment. The soil dwellers are absent. For most of the missing orders there can be noted characteristics of their habits, life histories or distributions that are or appear to be the limiting factors which account for their being absent from Hawaii. However, it is more difficult to explain why such groups as the cockroaches, for example, are not represented by native species. (It is noteworthy that endemic cockroaches exist on islands as far east as the Marquesas in southeastern Polynesia.)

Because of the lack of adequate, monographic, revisional studies, and because of my unfamiliarity with all of the pertinent details of the many genera of Hawaiian insects, the following summaries have been difficult to prepare. Some of the statistics given and conclusions reached will be subject to modification as more detailed and specialized work is done on both the Hawaiian and extra-Hawaiian faunas. Some of the genera which are listed as endemic may someday be found to have representatives elsewhere. Some of the species which are listed as endemic may be found to be immigrant or indigenous. For some of the genera which have been described as endemic to Hawaii, authors have neglected to say anything regarding their systematic positions, relationships, affinities or probable faunistic derivations. Such inconsiderate negligence is to be deplored. Some authors have "allied" Hawaiian genera to genera known to them from other localities, but in so doing, they have made errors that may persist for years in literature. Some of these errors will be carried along here, because it is obviously impossible to detect all of them. However, these opportunities for error are in the minority, and the

general conclusions should not be significantly influenced by them. This section is necessarily presented in an incomplete and tentative form; I am fully cognizant of its weak parts. I can only hope that the materials presented here will be food for thought and entice comment from scholarly specialists who may be able to aid us in our search for knowledge of Pacific insular life.

SUMMARIES OF THE ENDEMIC INSECTS

I. Summary of the Thysanura.—The only members of this primitive order which I consider possibly to be endemic are two species of *Machiloides* (Machilidae), but I am uncertain of their status. One of these species is known only from Kauai, but the other is widespread among the main islands. The group has received no attention since the original descriptive work by Silvestri in 1904. Both of the species have much in common with some of the Australian Machilidae, and it would not be surprising if these forms prove to be adventive.

II. Summary of the Orthoptera.—The 45 endemic forms are included in two families. The Tettigoniidae has two endemic genera: the monotypic *Conocephaloides* and *Banza* with 11 forms. The Gryllidae has 33 species included in four genera, three of which are endemic. *Paratrigonidium* (Indo-Pacific) has 16 species; *Prognathogryllus* (endemic) has 5 species; *Leptogryllus* (endemic) has 11 species; *Thaumtogryllus* (endemic) has 1 species. All of the endemic gryllid genera belong to a single assemblage and appear obviously to have sprung from a common ancestor. The affinities of the endemic Orthoptera are Indo-Pacific.

III. Summary of the Corrodentia.—It is difficult to summarize this order because of the chaos that exists regarding the status and relationships of genera and species. Enderlein has synonymized or reduced to varieties most of Perkins' species, but a careful, thorough revision is essential. For the purpose of this paper, I shall adopt the status of the species mainly as accepted by Perkins and Banks. (For references and details, see Volume 2 of this work.) The 24 species that appear to be native belong to the Psocidae and Elipsocidae. *Psocus* has 15 species (I have included the 14 species described in *Psocus* plus the single species described from a mutilated unique which Perkins placed in *Stenopsocus* but stated that it did not belong to that genus); *Kilauea* (endemic) has 8 species; *Palistreptus* (endemic) has 2 species. The other 16 species belonging to 13 genera all appear to be immigrants, although some of them are known only from Hawaii. Too little is known of the Corrodentia of the surrounding regions to enable a definite conclusion to be reached regarding the derivation of the Hawaiian fauna, but it appears to be southwestern Pacific in character.

IV. Summary of the Mallophaga.—Although there have been more than 50 species of Mallophaga recorded from Hawaii, few of them are endemic. Most of the species have been collected from domestic or introduced animals and sea birds. There never has been a careful search made for lice on the native birds, but a few species from some of them have been described. The Hawaiian lice are in great need of detailed study, for no definite conclusions can be reached with our present meager data. One would expect a wealth of interesting forms to

be found on the highly modified endemic Drepaniidae which might lend themselves to aiding in solving the problem of the relationship and derivation of those birds. I consider it a great scientific loss that such a survey was not made years ago when so much bird collecting was being done. Dr. Perkins made a collection of lice from endemic birds, but it appears to have been lost without ever having been studied. An ardent student might yet be able to find lice on museum skins of some of the extinct or very rare species, and a permit to collect a few specimens of the more common of the protected living species could probably be obtained for such a worthy study.

Although 19 species and varieties have been described from Hawaii, the only species which I now consider as having a claim to being endemic are five species found on drepaniid birds. These five species are: *Philoaterus macgregori* (Kellogg and Chapman), on *Chlorodrepanis virens*; *Degeeriella* (?) *diaprepes* (Kellogg and Chapman), on *Vestiaria coccinea*; *Myrsidea cyrtostigma* (Kellogg and Chapman), on *Chlorodrepanis virens*, *Himatione sanguinea* and *Vestiaria coccinea*; *Colpocephalum hilensis* (Kellogg and Chapman), on *Vestiaria coccinea*; and *Machaerilaemus hawaiiensis* (Kellogg and Chapman), on *Chlorodrepanis virens*.

There have been only three species out of the 62 kinds of endemic passerine birds from which lice have been described, and these three all belong to the Drepaniidae, which includes about 45 kinds of birds. No lice have been recorded from the endemic Sylviidae (warblers, 2 species), Turdidae (thrushes, 6 species), Corvidae (crows, 1 species), Muscicapidae (flycatchers, 3 species) or Meliphagidae (honey suckers, 5 species). No lice entirely confined to the endemic non-passerine birds (about 15 forms) have yet been found.

No conclusions can be drawn as to the relationships of the endemic Mallophaga at this time.

V. Summary of the Odonata.—There are 29 forms of endemic Hawaiian Odonata. These have come from three stocks. The first of these is the single species of Libellulidae, which has been separated as a "weak" Hawaiian genus from the Holarctic genus *Sympetrum* and is now called *Nesogonia blackburni* (McLachlan). The second stock is that represented by the giant endemic *Anax strenuus* Hagen, an apparent offshoot of the cosmopolitan species *Anax junius* (Drury) of the Aeshnidae. The remaining 27 forms constitute the endemic damselfly complex *Megalagrion* of the Coenagriidae. It is apparently only a matter of taxonomical convenience that the Hawaiian species are separated as a distinct genus from the Oriental-Pacific genus *Pseudagrion*. Thus, only three ancestral individuals have given rise to all of the Hawaiian Odonata. The extensively developed *Megalagrion* complex is of great interest, because some of the species have forsaken streams and ponds and habitually breed in little pockets of water at the bases of the leaves of certain kinds of forest plants; one is even more aberrant, for it is terrestrial and lives in damp trash under ferns far from water.

VI. Summary of the Thysanoptera.—There have been about 90 thrips recorded from Hawaii, but most of these are immigrants. Unfortunately, the Hawaiian Thysanoptera have not been carefully revised, and it is difficult for one unfamiliar

with the group to draw many concrete conclusions. From present knowledge, it appears to me that there may be only about six or fewer genera which contain endemic species. There are 15 species of *Hoplothrips* (Tubulifera: Phlaeothripidae) which appear to be endemic. *Nesothrips* (Tubulifera: Phlaeothripidae), known from the Indo-Pacific, contains one possibly native form. *Dermothrips* (Phlaeothripidae) and *Conocephalothrips* (Urothripidae), both monotypic, may be native. *Haplothrips* (Phlaeothripidae) contains four species which may be endemic. There are seven species of *Isoneurothrips* (Terebrantia: Thripidae) which may be endemic. Although there are several species not yet recorded from outside Hawaii, and even some genera which have been described as new from Hawaii, there is no good evidence to indicate that some of these are not immigrants. As is true for the endemic thrips faunas of Fiji, Samoa and other Polynesian islands, there is a preponderance of Tubulifera, which are frequently met with beneath dead bark of shrubs and trees, and a dearth of flower-frequenting species. The endemic forms are evidently normal derivatives of Pacific faunas.

VII. Summary of the Hemiptera-Heteroptera.—There have been 223 kinds of Heteroptera listed from Hawaii, including 178 endemics. The greatest development and diversity of some genera occur in Hawaii, and a number of distinct genera and groups of allied genera are remarkable endemic products. Many new species are known and await description. Because there are so many endemic forms, I shall discuss each family separately.

1. Pentatomidae. The largest, most conspicuous and brightly colored of all endemic Heteroptera is a single species of *Coleotichus* which is widely distributed in the islands. The genus is Indo-Pacific in distribution. The genus *Oechalia* has 15 described species. Of these, only one species has been found outside of Hawaii, and it is widespread in many islands from Australia to eastern Polynesia but has not reached Hawaii. The 14 Hawaiian species are placed in the endemic subgenus *Hawaiicola*.
2. Coreidae. Two endemic species belonging to the endemic genus *Ithamar* compose the native Coreidae. *Ithamar* is an ally of *Daclera* and is of Indo-Pacific origin.
3. Lygaeidae.
 - (a). The tribe Orsillini of the Lygaeinae with its 67 endemic species, 14 endemic subspecies and 3 endemic varieties is evidently the largest tribal unit of the Hawaiian Heteroptera. These forms are included in five genera and five subgenera: *Occanides* (23 species), *Glyptonysius* (2 species), *Neseis* [with subgenera *Physonysius* (2 species), *Leionysius* (2 species), *Neseis* (1 species), *Trachynysius* (13 species, 12 subspecies, 2 varieties), *Icteronysius* (2 species)], *Nysius* (21 species, 2 subspecies, 1 variety) and *Nesomartis* (1 species). All of these genera and subgenera are endemic except the almost cosmopolitan genus *Nysius*. The species of *Nysius* are, however, all endemic and include the most divergent of all *Nysius* species. The tribe, as a whole, has its greatest known diversity in Hawaii. The entire Hawaiian group may have been derived from about seven, or fewer,

immigrant ancestors from the south and western Pacific.

(b). The Metrargini of the Lygaeinae constitute an endemic tribe including the three endemic genera *Metrarga* (1 species, 2 varieties), *Nesoclimacias* (1 species, 2 varieties) and *Nesocryptias* (1 species). It appears that all of these forms could have been derived from a single immigrant ancestor from the same region as the Hawaiian Orsillini. It may be an aberrant local offshoot of some ancient Hawaiian orsilline type.

(c). The Cyminae include two allied, endemic monotypic genera, *Sephora* and *Nesocymus*. These are apparently derivatives from a common Indo-Pacific immigrant, and new species await description.

4. Enicocephalidae. One supposedly endemic species of *Nesenicoccephalus* known only from a single specimen from Maui represents this family. The recently described genus is known only from the Philippines and Hawaii.
5. Reduviidae. One species of the endemic *Nesidiolestes* (Ploiariinae), allied to other genera which are widespread in the Indo-Pacific, is probably the only described endemic species of this family in Hawaii.
6. Nabidae. There are 25 endemic species described from Hawaii. These belong to the widespread genus *Nabis*. All of the endemic forms are so closely allied that perhaps a single immigrant from the south Pacific has accounted for the present endemic complex.
7. Anthocoridae. The six described endemic species are included in *Lasiochilus* (5 species) and *Lilia* (endemic, monotypic), and their relationships are Indo-Pacific.
8. Miridae. This family now comes next to the Lygaeidae in its development and diversification in the islands. It contains 27 endemic species, 1 variety and 9 endemic genera described, but a large number of undescribed forms are in our collections, and when they are described this family is expected to outnumber the Lygaeidae. Our representatives are all considered Pacific derivatives.

(a). The endemic Phylinae are included in the nearly cosmopolitan genus *Psallus*. There are four species and a variety described from Hawaii, but more native species await description.

(b). The Dicyphinae includes only two described endemic species of the widespread genus *Engytatus*, but many species remain to be described.

(c). The Bryocorinae is represented by four described species of the endemic genus *Sulamita* and by the monotypic, endemic *Kalanina*. These genera are here placed in endemic tribes.

(d). The Heterotominae includes the endemic, monotypic *Nesidiorchestes* and *Sarona*, *Pseudoclerada* (endemic, 2 species, here considered a native tribe), *Orthotylus* (widespread, 7 Hawaiian species described, but many new ones at hand), *Kamehameha* (endemic, monotypic derivative (?) of *Orthotylus*), *Koanoa* (endemic, 2 species).

(e). The endemic, monotypic genera *Oronimiris* and *Nesiomiris* represent the Mirinae, but many new species are in collections and await description.

9. Saldidae. This family is represented in the islands by six described endemic species of *Saldula*, but new species await description. Evidently these species represent derivatives of a common Polynesian ancestral stock.
10. Gerridae. The pelagic water striders are represented by two species of *Halobates*, one of which appears to be endemic, the other indigenous.

These 10 families represent only about 20 percent of the families of Heteroptera (in deriving this and similar percentages, I have used the total number of families as given by Brues and Melander in 1932). Moreover, only the four families Pentatomidae, Lygaeidae, Anthoridae and Miridae have more than a single genus containing native species represented in Hawaii. Four of the families are each represented by only a single native species. It will be noted that the aquatic forms are hardly represented, and that none of the families of fresh-water diving bugs is present. The entire bug fauna is strikingly insular.

VIII. Summary of the Hemiptera-Homoptera.—There have been over 500 species of Homoptera recorded from the Territory. However, more than 160 of these species are immigrants. The only families of the Homoptera that have proven endemic species in the Hawaiian Islands are the Pseudococcidae, Cicadellidae, Delphacidae, Cixiidae and Psyllidae, and I have listed 341 of these as native. These five families make up only about 8 percent of the families of Homoptera.

1. Cicadellidae. There are two species included in the endemic genus *Nesophrync*, which appears to resemble the Eurasian genus *Goniagnathus* and which is allied to our *Kirkaldiella* and *Nesophrosync*. *Kirkaldiella* (endemic derivative of *Nesophrosync*) has two species; *Nesophrosyne* (endemic; probably a derivative of the *Thamnotettix* complex) has 62 forms; *Balclutha* (*Nesosteles*) (well developed in the Pacific) has five native species and *Nesolina*, which may be a local endemic development, is monotypic. This group is Indo-Pacific in affinities.
2. Delphacidae. There are 139 endemic forms placed in the following genera: *Leialoha* (endemic, 12 species); *Nesothoë* (endemic, 22 species); *Nesodryas* (endemic, 2 species); *Aloha* (endemic, 9 species); *Nesorestias* (endemic, 2 species); *Nothorestias* (endemic, 2 species); *Dictyophorodelphax* (endemic, 4 species); *Nesosydne* (endemic, 82 species); *Kelisia* (5 endemic species). With the exception of the species of *Kelisia*, all of these genera belong to a group called Alohini by Kirkaldy. Two or three ancestral immigrants from the southwest Pacific could have given rise to the entire family in Hawaii. Some of the most remarkable endemic products are included in this family.
3. Cixiidae. There are 84 endemic forms in this family. Seventy-nine of these belong to *Oliarus* and five to *Iolania*. *Iolania* was described as an endemic genus, but it is now known from Fiji also. *Iolania* may be an offshoot of the widespread genus *Cixius*. Two Pacific ancestral stocks appear to be represented by this group.
4. Psyllidae. There have been 30 species and one variety of jumping plant lice described as endemic. These species are distributed as follows: *Swezey-*

ana (endemic, 2 species); *Paurotriozana* (endemic, 1 species); *Trioza* (9 species); *Kuwayama* (5 species, 1 variety); *Hevaheva* (endemic, 9 species); *Megatrioza* (1 species, but several other undescribed species are at hand); *Cerotrioza* (endemic, 2 species); *Crawforda* (endemic, 1 species). Most of these species are related to *Trioza* and might have sprung from a single immigrant ancestor. Perhaps two original southwestern Pacific immigrants representing the genera *Trioza* and *Cerotrioza* gave rise to the Hawaiian complex.

5. Pseudococcidae. We have now shown beyond a doubt that Hawaii has a peculiarly developed mealybug fauna of its own. The endemism as we interpret it is as follows: *Phyllococcus* (endemic, monotypic), relationships undetermined, an unusual form; *Clavicornis* (endemic, 2 species), another striking group, evidently an old local development; *Pseudococcus* (9 species); *Trionymus* (1 species); *Nesococcus* (endemic, monotypic), another local offshoot, possibly of an old *Pseudococcus* form. Although we are unable to say at this time exactly where the closest affinities of the Hawaiian group lie, it is suggested that perhaps three or four immigrant Indo-Pacific stocks might have given rise to this faunal element.

IX. *Summary of the Neuroptera*.—There have been 60 species of Neuroptera recorded in Hawaii. Of these, 54 are endemic species; the remainder are either purposely or accidentally imported species. The endemic species are included in three families which represent only 15 percent of the known families of Neuroptera.

1. Myrmeleontidae. One species of *Eidoleon* is considered endemic. It is closely allied to a south Pacific species.
2. Chrysopidae. Twenty-six species belonging to the endemic genus *Anomalochrysa* have been described. The genus appears to have allies in Samoa, and seems to have developed in Hawaii from a single ancestral immigrant.
3. Hemerobiidae. The 28 endemic species are included in four genera as follows: *Nesobiella* (endemic (?), monotypic); *Nesomicromus* (endemic, 22 species); *Pseudopsectra* (endemic, 4 species); *Nesothauma* (endemic, monotypic). The five species last mentioned are flightless and have greatly reduced and modified fore wings, and the hind wings are atrophied and minute or absent. These are among the most aberrant of all Neuroptera, but are obvious local offshoots of *Nesomicromus*. Probably two immigrant Polynesian ancestors could have given rise to the endemic Hemerobiidae, or one if the *Nesobiella* proves to be non-endemic.

X. *Summary of the Lepidoptera*.—There have been approximately 1,000 species of Lepidoptera recorded from the islands. Hereinafter I have listed 850 species and 10 varieties of these as endemic forms. These are included in 21 families which amount to only 15 to 20 percent of the families of Lepidoptera. None of the primitive families is represented.

This review has revealed to me that chaos exists in the classification of the Lepidoptera. The Hawaiian group is in great confusion and is most difficult to

work with in its present state. There are many erroneous generic and family assignments. Often none of the several authors who have worked upon a particular group agrees upon the position or relationships of the included insects. There appear to be numbers of misidentifications. Some of the published material is useless for the purpose of this paper because of errors and omissions. Unfortunately, I am unfamiliar with the order and cannot weigh evidence and correct errors which an authority on the order might do if he were particularly interested in this problem. Before any satisfactory analysis of the Hawaiian Lepidoptera can be attempted, careful revisions must be made of all of the groups of the order represented in Hawaii in the broad light of geographical distribution, derivation and evolution. Moreover, a more accurate and complete knowledge of the faunas of the south Pacific must be attained. I must admit that this section of the paper has many weak spots.

1. Gelechiidae. *Aristotelia* has 16 endemic species. This cosmopolitan genus is evidently poorly represented elsewhere in Polynesia, for there is only a single species recorded, and that is from Samoa. The affinities of the Hawaiian species have not been determined beyond their being considered Pacific. *Merimnetria* appears to be endemic and monotypic, and, although considered a Pacific derivative, it is of uncertain status.
2. Cryptophasidae. *Thyrocopa* (endemic, affinities unknown) has 34 endemic species. From this genus there appear to be five endemic generic segregates: *Hodegia* (monotypic), *Ptychothrix* (monotypic), *Diplosara* (monotypic; an aberrant form), *Psychra* (2 species) and *Catamempsis* (monotypic). These six groups evidently arose from a single immigrant. *Hodegia* is peculiar, because the female is flightless (the male is unknown), has greatly reduced wings and is a jumping insect found in bunch grass high up in the open country of Haleakala, Maui. These are considered south Pacific derivatives.
3. Cosmopterygidae. *Agonismus* (endemic; an ally of *Hyposmocoma*) has 3 species; *Aphthonetus* (endemic; allied to *Hyposmocoma*) has 33 species; *Rhinomacrum* (endemic; allied to *Aphthonetus*) has 2 species; *Neelysia* (endemic derivative of *Hyposmocoma*) has 25 species; *Dysphoria* (endemic ally of *Hyposmocoma*) is monotypic; *Bubaloceras* (endemic; allied to *Hyposmocoma*) has 2 species; *Hyposmocoma* (endemic; an ally (?) of the nearly cosmopolitan *Mompha*) contains more described species than any other Hawaiian genus, for it has 210 species and 6 varieties; *Euhyposmocoma* (endemic offshoot of *Hyposmocoma*) has 2 species; *Hyperdasysella* (= *Hyperdasys*) (endemic ally of *Hyposmocoma*?) has 5 species; *Pthoraula* (endemic derivative of *Hyposmocoma*) is monotypic; *Euperissus* (endemic; supposedly allied to *Orthotaenia*) has 2 species; *Semnoprepia* (endemic; closely allied to *Euperissus*) has 7 species; *Petrochroa* (endemic; supposedly allied to *Coelopoeta*) has 6 species.

There appear to be only three ancestral stocks necessary for the origin of the endemic Cosmopterygidae. One has apparently given rise to

Hyposmocoma and 9 allied genera including 290 forms; one evidently produced *Euperissus* and *Scmnoptrepia* with 9 species; and the third gave rise to *Petrochroa* with 6 species. In addition to these, there are 2 endemic species incorrectly assigned to *Elachista* which are now of uncertain status, but which may also belong to the *Hyposmocoma* complex. These are all considered Pacific derivatives.

4. Tineidae. *Comodica* (Samoa, Australia, etc.) has 1 apparently (?) endemic species; *Ereunetis* (well developed in Samoa and elsewhere) has 5 apparently endemic species and several immigrants. *Paraphasis* (endemic; of uncertain status) is monotypic.
5. Yponomeutidae. *Mapsidius* (endemic; of undetermined affinities) has 4 species; *Acrolepia* (almost cosmopolitan) has 3 species of undetermined derivation.
6. Nepticulidae. *Opostega* (almost cosmopolitan) has 6 species of undetermined derivation.
7. Batrachedridae. *Batrachedra* has 9 species evidently of south Pacific derivation.
8. Caloptiliidae. *Parectopa* has 15 species evidently of western Pacific derivation.
9. Bedelliidae. There are 3 species of *Bedellia* which may be endemic and are probably of south Pacific derivation.
10. Orneodidae. *Ornecodes* has 2 species possibly of western Pacific derivation.
11. Tortricidae. *Eccoptyocera* (endemic; supposedly allied to *Holocola* of Australia, but status uncertain) is monotypic (immigrant ?); *Gypsonoma* has 1 species evidently with western Pacific affinities; *Adcnoneura* (endemic; ally of *Eucosma* [*Thiodia*]) has 8 species of undetermined affinities; *Spheterista* (perhaps a derivative of *Capua*) has 4 species; *Bactra* (western Pacific affinities ?) has 3 species; *Pararrhaptica* (endemic; affinities uncertain) is monotypic; *Enarmonia* (widespread) has 4 species; *Eulia* (widespread) has 17 species; *Panaphelix* (endemic; ally of *Dipterina*) has 2 species; *Dipterina* has 1 species with south Pacific affinities; *Tortrix* (widespread) has 7 species; *Capua* has 13 species probably of south Pacific derivation; *Epagoge* has 5 species evidently of western Pacific affinities. Following Walsingham (1907), I list the Tortricidae as all belonging to the Indo-Pacific fauna.
12. Carposinidae. *Carposina* has 38 species and 2 varieties probably of south Pacific derivation.
13. Crambidae. *Prionopteryx* has 1 species possibly of south Pacific derivation; *Talis* has 6 species which appear to be allied to the Australian section of the genus.
14. Phycitidae. *Rhynchephestia* (endemic, of undetermined affinities) has 1 species; *Genophantis* (endemic; allied to *Crocodyopora*) has 2 species with southwestern Pacific affinities; *Homocosoma* has 3 species apparently allied to Australian species.

15. Pyraustidae. *Margaronia* (abundant on many Polynesian islands) has 2 species; *Omiodes* has 23 species with southwestern Pacific affinities; *Phlyctaenia* has 27 species with southwestern Pacific derivation; *Pyrausta* has 11 species with western Pacific affinities; *Tholeria* (*Mecyna*) has 2 species possibly (?) with North American affinities; *Loxostege* has 3 species with North American (?) affinities; *Promylaea* (endemic; closely allied to *Mestolobes*) has 2 species; *Mestolobes* (endemic, with south Pacific affinities, others known from the Marquesas) has 32 species; *Orthomecyna* (endemic; allied to *Mestolobes*) has 14 species; *Protaulacistis* (endemic; allied to *Mestolobes* and *Orthomecyna*) is monotypic; *Scoparia* has 64 species of south Pacific derivation; a number occur in the Marquesas.
16. Pterophoridae. *Platyptilia* (widespread) has 5 species which may be endemic and are Pacific in affinities.
17. Sphingidae. *Celerio* has 2 species and a variety which appear to have arisen from one ancestral stock—perhaps *Celerio galli* from North America. *Protoparce* has a variety (subspecies ?) of a common widespread species. The affinities of these large, strong-flying moths appear to be with North America. I have excluded the monotypic *Tinostoma*, which is said to be allied to the American *Pholus*. The only known example was collected about a half century ago in a dwelling on Kauai, and in spite of specialized searching no additional specimens have been found. I feel that it is possible that this species is an immigrant which might have been carried to the place of capture as a pupa in imported merchandise.
18. Geometridae. *Sisyrophyta* (endemic offshoot of *Scotorythra*) has 2 species; *Nesoclide* (endemic derivative of *Scotorythra*) is monotypic; *Scotorythra* (endemic; of south Pacific origin) has 36 species; *Tritocleis* (endemic offshoot of *Scotorythra*) is monotypic; *Eucymatoge* has 10 species of western Pacific or Asiatic derivation; *Hydriomena* has 4 species of western Pacific or Asiatic derivation; *Xanthorhoe* has 3 species of south Pacific derivation; *Prognostola* has 1 species with south Pacific affinities; *Dasyuris* has 1 species of south Pacific derivation.
19. Phalaenidae (Noctuidae, Agrotidae). *Eriopygodes* has 1 variable species with western (?) Pacific affinities; *Hyssia* has 3 species of south (?) Pacific derivation; *Acrapex* has 1 species with Oriental affinities; *Agrotis* has 29 species which appear to be of Asiatic derivation; *Autographa* (widespread) has 7 species with undetermined affinities; *Hypocala* has 1 species allied to south Pacific and Australian species; *Hypernodes* (endemic; with western Pacific affinities) has 7 species; *Prodenia* has 1 species of south Pacific origin; *Nesamiptis* (endemic; with North American affinities) has 6 species; *Cosmophila* has 3 species of western Pacific affinities; *Cirphis* has 3 species with North American (?) affinities which may be endemic; *Peridroma* has 6 species which appear to be Asiatic derivatives.

20. Nymphalidae. *Vanessa* has a single species which apparently is a North American derivative.
21. Lycaenidae. *Lycaena* has a single species which is apparently a western Pacific or Asiatic derivative. Its larva is unusual in that it lacks dorsal glands.

XI. *Summary of the Coleoptera*.—There have been more than 1,600 species of beetles listed from Hawaii. Of these, I have included 1,220 species and 70 varieties as endemic to the Territory. These species are included in 19 families which total only about 11 percent of the families of Coleoptera.

1. Carabidae. This family is one of the most extensively developed of any in the native fauna, for it contains 222 species. A revision of the group is in progress; many of the genera are being combined and others are being reduced to subgeneric rank.

In the Bembidiini, *Bembidion* has 5 species, some of which may prove to be immigrants. From an early *Bembidion* ancestor have arisen *Nesociidium* (endemic) with 10 species, *Nesomicrops* (endemic) with 1 species, *Macranillus* (endemic) with 1 species, *Atelidium* (endemic) with 1 species and *Metrocidium* (endemic) with 1 species. The seemingly aberrant, endemic, monotypic genus *Gnatholymnaeum* appears to be closely allied to the North American *Amerizus*, according to E. B. Britton (personal communication). The endemic Bembidiini appear to have arisen from two or three Holarctic stocks, but it is not now known whether they came from America or Asia or two from Asia and the other from America.

All the Nomiini at one time were considered to belong to the endemic genera *Mecyclothorax*, *Atelothorax*, *Thriscothorax* and *Metrothorax*, but we do not recognize these as distinct units now, and the entire group is merged with the Indo-Australian *Cyclothorax* under the name *Mecyclothorax*. All of the Hawaiian species are flightless, but some Australian *Cyclothorax* have well-developed wings. This genus is now known from Tahiti (4 species), New Caledonia (1 species), New Zealand (1 species), Australia (15 species), Java (3 species), St. Paul and Amsterdam (south Indian Ocean) (1 species) and Hawaii with 85 described species.

The Anchomenini are the most extensively developed group. They are derivatives of *Colpodes*, a genus widespread and well developed in the Pacific. In an unpublished manuscript, many of the following genera are being synonymized, but Sharp's classification (1903) is used here. *Atrachycnemis* (endemic ally of *Blackburnia*) has 3 species; *Blackburnia* (endemic) has 2 species; *Deropristus* (endemic ally of *Blackburnia*) has 3 species; *Anchotefflus* (endemic ally of *Blackburnia*) has 2 species; *Pseudobroschus* (endemic ally of *Disenochus*) is monotypic; *Derobroschus* (endemic ally of *Pseudobroschus*) has 3 species; *Disenochus* (endemic) has 13 species; *Mauna* (endemic offshoot of *Disenochus*) is monotypic; *Brosconymus* (endemic derivative of *Disenochus*) is monotypic; *Aptero-mesus* (endemic ally of *Disenochus*) is monotypic; *Mysticomenus* (en-

demic offshoot of *Apteromesus*) has 2 species; *Colpodiscus* (endemic ally of *Disenochus*) has 2 species; *Anchonymus* (endemic ally of *Disenochus*) is monotypic; *Prodisenochus* (endemic ally of *Disenochus*) is monotypic; *Barypristus* (endemic ally of *Disenochus*) has 2 species; *Baryneus* (endemic offshoot of *Barypristus*) is monotypic; *Chalcomenus* (endemic ally of *Barypristus*) has 3 species; *Colpodes* (incorrectly assigned to *Platynus* in *Fauna Hawaiiensis*) has 2 species; *Metromenus* (endemic ally of the endemic *Colpodes* species) has 28 species; *Mecomenus* (endemic ally of *Metromenus*) has 2 species; *Colpocaccus* (endemic ally of *Metromenus*) has 6 species; *Atelothrus* (endemic ally of *Metromenus*) has 19 species and 1 variety; *Mecostomus* (monotypic, endemic ally of *Metromenus*); *Mesothriscus* (endemic ally of *Metromenus*) has 14 species and 2 varieties. One or two ancestral immigrants from the southwest Pacific are considered to have given rise to this entire closely knit complex.

It now appears to me that the entire endemic carabid fauna could have developed from only about four to six ancestral immigrant species.

2. Dytiscidae. One species of *Rhantus* and one of *Copelatus* appear to be endemic representatives of this family of water beetles. Both species are south Pacific derivatives.
3. Staphylinidae. *Thoracophorus* (endemic) has 2 species; *Lispinodes* (endemic) has 10 species; *Myllaena* (nearly cosmopolitan) has 11 species. The 28 species and 1 variety of Hawaiian *Oligota* (cosmopolitan) have been separated into 5 subgenera as follows: *Dcroligota* (endemic) monotypic, *Holobus* has 1 species, *Gnatholigota* (endemic) has 5 species, *Nesoligota* (endemic) has 7 species, *Oligota* has 14 species and 1 variety; *Liophacna* (endemic; closely allied to *Oligota*) has 3 species. It is probable that all of these forms have sprung from a single immigrant. I am not convinced that the species placed in subgenera found elsewhere are typical of them, nor do I believe that they necessarily have anything more in common than generic relationship. The derivation of the Hawaiian complex is undetermined, but I consider an Indo-Pacific origin indicated. *Eudicstota* (endemic ally of *Dicstota*) is monotypic; *Dicstota* (widespread) has 29 species; *Eusipalia* (endemic ally of *Dicstota*) is monotypic. It appears probable that the 31 species included in these last three genera have arisen from a common ancestral immigrant; the source is not known, but it is presumed to be Pacific. *Nesomedon* (endemic derivative (?) of *Medon*, cosmopolitan) has 3 species. *Xanthocorynus* (monotypic), *Holocorynus* (2 species) and *Leurocorynus* (monotypic) are three allied endemic genera all said to be allied to *Leptacinus* and *Pachycorynus* and are probably of south Pacific derivation.
4. Histeridae. The only endemic species in this family appear to be 32 species and 3 varieties of *Acritus*. The genus is nearly world-wide, but it is too poorly known to enable us to ascertain the affinities of the Hawaiian species at this time. From what I know of the histerid faunas

of south Pacific islands, I would suggest that it is probable that the Hawaiian forms are of south Pacific derivation.

5. Nitidulidae. The 133 endemic species and 10 endemic varieties of this family form a remarkable assemblage. There are two main stocks present. The first of these is a great complex of 11 endemic genera containing 129 species and 10 varieties. The other stock is represented by two genera including four species. I do not feel that this group as it now stands should be split up into so many loosely defined genera.

The first of these groups is composed of *Goniothorax* (9 species), *Gonioryctus* (22 species, 1 variety), *Nesapertus* (2 species), *Eunitidula* (monotypic), *Orthostolus* (10 species), *Cyrtostolus* (monotypic), *Apeta-sinus* (monotypic), *Apetinus* (5 species), *Eupetinus* (24 species, 7 varieties), *Nesopeplus* (31 species) and *Nesopetinus* (23 species, 2 varieties). This entire complex of closely allied forms has evidently been derived from a common ancestral immigrant of *Brachypeplus*, a genus well developed in the southwest Pacific.

The other section has two genera: *Notopeplus* (monotypic) and *Cil-laeopeplus* (3 species). These genera were described as endemic. However, I have undescribed species of *Notopeplus* before me from the Marquesas. These genera also appear to be derivatives of *Brachypeplus*.

6. Cucujidae. The two genera containing endemic species are *Brantolacmus* (endemic) with 4 closely allied species and 3 varieties, and *Lacmophloeus* (*Parandrita*) with 6 closely allied "species." The *Lacmophloeus* forms may have to be placed in a new genus. This assemblage is here considered Indo-Pacific in origin.
7. Dermestidae. The endemic species are included in three allied genera: *Labrocerus* (endemic; 17 species), *Agrocerus* (endemic; 2 species) and *Eocerus* (endemic; monotypic). These genera and species appear to be derivatives of an ancestral immigrant *Trogoderma* which possibly came from the south Pacific.
8. Hydrophilidae. Two species of *Limnoxenus* with south Pacific affinities appear to be endemic.
9. Anobiidae. The 137 endemic species and 19 endemic varieties are included in three genera. *Mirosternus* has 70 species and 1 variety (originally described as endemic, but it is now also known from the Seychelles and Ceylon); some Central American species were formerly incorrectly assigned to it (see Scott, 1924:368); the genus *Dorcatomiella* of southern Polynesia appears to be a close ally. *Xyletobius* (endemic) has 53 species and 16 varieties. *Holcobius* (endemic ally of *Xyletobius*) has 14 species and 2 varieties. The Hawaiian Anobiidae are considered to be Indo-Pacific derivatives.
10. Ciidae. The cosmopolitan genus *Cis* is represented by 35 endemic species and 1 endemic variety. These forms perhaps are polyphyletic and may

have arisen from three independent immigrants. The derived genus *Apterocis* is an endemic, flightless complex of 13 species and 1 variety. A south Pacific origin for the entire group is probable.

11. Elateridae. *Eopenthes* is an endemic genus of 33 species and 1 named variety. It appears to be related to the Pacific *Melanoxanthus* complex which has *Pacificola* so well developed in the Marquesas. *Itodacnus*, an endemic ally of *Eopenthes*, has 9 species. *Dacnitus*, an endemic derivative of *Itodacnus*, is monotypic. *Anchastus* has 1 apparently endemic species whose affinities lie with the Fijian and western Pacific species.
12. Eucnemidae. *Dromaeolus* has 31 species and 1 variety endemic. The endemic, monotypic *Ceratotaxia* is probably a derivative of *Dromaeolus*. The members of this family could have developed from an ancestral immigrant from the south Pacific.
13. Alleculidae. There are 5 endemic species of *Pseudocistela* and 3 of *Labetis*, an allied, endemic genus. *Pseudocistela* is almost cosmopolitan, and our species may be allied to those of the southwest Pacific.
14. Cerambycidae. The 100 endemic Cerambycidae are among the most remarkable of all the endemic insects. They have been derived from three stocks. *Parandra* has a single species which closely resembles the Fijian species. *Mcgopsis* (*Aegosoma*) has one endemic species derived from the western Pacific. The remainder of the endemic Cerambycidae are grouped in and around *Plagithmysus*, and have evidently all arisen from an ancient immigrant ancestor allied to or belonging to the widespread *Neoclytus* (Dr. W. H. Anderson and Dr. Fritz Van Emden inform me that the larvae are hardly distinguishable from *Neoclytus*). Whence this ancestral stock came is not known. It is one of those early Hawaiian stocks whose affinities are now most difficult to trace, but it appears that these beetles are of North American origin.

Plagithmysus has 55 species and 2 varieties, *Neoclytarlus* has 26 species and 1 variety, *Callithmysus* has 2 species and 1 variety, *Paraclytarus* has 5 species, *Nesithmysus* has 4 species and *Aeschrithmysus* has 2 species. All of these genera are endemic, are closely allied to one another and all appear to have sprung from a single introduction.

15. Anthribidae. Two species of endemic *Araccerus* of south Pacific derivation represent the Anthribidae.
16. Aglycyderidae (Proterhinidae). The genus *Proterhinus* contains 164 endemic species and 17 varieties (or subspecies?). The genus was long considered to be restricted to Hawaii, but new species have since been described from Samoa and the Phoenix and Marquesas Islands. I have collected new species in the Society and Austral Islands and have a new species from Fiji. The Samoan species also occurs in Fiji and is fully winged, whereas all the Hawaiian species are flightless. The other

known species of the family are found as follows: two in New Zealand, one in New Caledonia and one in the Canary Islands.

17. Curculionidae. *Rhyncogonus* was described first from Hawaii where there are 34 described species. The genus is now known from the Cook, Austral, Society, Tuamotu and Marquesas archipelagos as well as from Christmas, Fanning and Wake atolls. The genus is more highly developed in southeastern Polynesia than in Hawaii, and it belongs to a tribe (Celeuthetini) which is greatly developed in the western Pacific.

There have been 22 endemic species assigned to the supposedly cosmopolitan genus *Acalles*. They will probably prove to be western Pacific or Asiatic derivatives through a common ancestral immigrant. *Chaenosternum* is a monotypic, local endemic derivative of some endemic *Acalles*.

Dryophthorus is nearly cosmopolitan, but the 17 endemic Hawaiian species are more than are found in any one other locality. The Hawaiian species appear to have affinities with the species of Samoa and Fiji. *Stenotrupis* has two endemic species which are south Pacific derivatives. *Orothreptes* has not been recorded outside of Hawaii, but I know it from the Marquesas. Its single species may be indigenous instead of endemic. *Nesotocus* is evidently a relict endemic genus of four closely allied species, and there appears to be nothing like it elsewhere. I have suggested that it appears that it may be of western Pacific origin. *Oodemas* with its 58 species and three varieties is the largest genus of the Hawaiian Cossoninae. This genus, together with its close ally *Anothecorus* (three species), is endemic, and I know of no genus or group of genera from any region from which it might have come. It is an anomaly. *Heteramphus* has 12 species and *Dysomma* is monotypic; both genera are peculiar endemics. These two genera, which are allied, are in the same category as *Oodemas* and *Nesotocus*, for they are apparently without living ancestors. However, I have certain undescribed weevils from the south Pacific which may shed some light on the possible affinities of the group. *Deinocossonus* is endemic and monotypic, but it or allied genera may possibly yet be found in the south Pacific.

These weevil genera belong to only three (Otioryhynchinae, Cryptorhynchinae and Cossoninae) of the more than 70 subfamilies of Curculionidae! The Curculionidae appears to be the largest family of organisms, and although approximately 40,000 species have been described, the group is poorly known.

18. Scolytidae. Although there have been a number of minute Scolytidae described from the islands in such genera as *Hypothenemus*, it appears to me that these have little claim of endemism. For the present, then, I shall include in this list only the members of the genus *Xyleborus* which are considered to be endemic. The genus *Xyleborus* is widespread, but the Hawaiian group of about 22 species and one variety may possibly have been derived from the south Pacific.

19. Lucanidae. On the island of Kauai there exists the aberrant, endemic genus of flightless stag beetles, *Apterocyclus*. It is polymorphic, and what were at one time considered to be seven species are now thought to represent one species and two varieties. The genus is evidently an aberrant derivative of Oriental *Dorcus*, and it is the only Hawaiian representative of that great series of beetles known as the Lamellicornia, which is so greatly developed on all the continents and most continental islands.

XII. *Summary of the Hymenoptera*.—There have been nearly 1,000 species of Hymenoptera recorded from the Territory, but many of these are immigrants or purposely introduced species. Herein I have listed 618 as native insects.

1. Ichneumonidae. *Agrypon* (*Atrometus*) has 11 species evidently derived from the western Pacific (these may belong to a new genus); *Echthromorpha* has 1 species of south Pacific affinity; *Enicospilus* is the most highly developed of the local Ichneumonidae, for it contains 17 species of south Pacific derivation in addition to the endemic subgenus *Glyptogastra*, which contains 2 species; *Ercmotyloides* is an endemic derivative of *Enicospilus* containing 3 species; *Banchogastra* (endemic ally of *Enicospilus*) has 2 species; *Pleuroncuropion* (endemic segregate of *Enicospilus*) has 2 species; *Pycnophion* (endemic ally of *Enicospilus*) has 3 species; *Abanchogastra* (endemic ally of *Enicospilus*) has 2 species. Excepting *Agrypon* and *Echthromorpha*, all of these endemic species belong to the one tribe, Ophionini.

(Braconidae. All of the Braconidae with the possible exception of the possibly endemic genus, or species of, *Ecphylopsis*, of undetermined affinity and which contains a single species, are evidently foreign insects. The status of this insect is so uncertain that I have omitted it from the tabular summary.)

2. Encyrtidae. *Anagyrus* (widespread) has about 7 native species described, and others known but undescribed; *Coelopencyrtus* (endemic; affinities undetermined) has 4 species; *Hypergonatopus* (endemic; ally of *Echthrogonatopus*, and evidently of south Pacific derivation) has 7 species; *Xanthoencyrtus* (subgenus *Mirastymachus*) widespread, has 6 species endemic. I consider all of these Pacific derivatives.
3. Eupelmidae. *Eupelmus* (widespread) contains 54 described native species and a number of undescribed species. *Lepideupelmus* (endemic derivative of *Eupelmus*) has 3 species. These have Pacific affinities.
4. Miscogasteridae. All of the native species belong to the Lelapinae. *Toxeuma* (widespread) has 6 species; *Neolelaps* (endemic) is a monotypic offshoot of *Toxeuma*, if distinct; *Calolelaps* (endemic; ally of *Neolelaps*) has 2 species; *Stictolelaps* (endemic; ally of *Neolelaps*) has 3 species; *Mesolelaps* (endemic; ally of *Neolelaps*) is monotypic. These species are of unknown derivation but they differ from the American Lelapinae and are here considered Pacific derivatives.

5. Spalangidae. One species of *Spalangia* with south Pacific affinities may be endemic.
6. Aphelinidae. *Ophelinus* has 2 species with southwestern affinities.
7. Eulophidae. It is difficult to ascertain which, if any, of the species are positively endemic, but the following may be native: *Eulophus* (widespread) has 1 species; *Hemiptarsenus* (widespread) has 1 species; *Necremnus* has 1 species of undetermined derivation; *Sympiesis* (widespread) has 1 species. Perkins (1913:cvi) said that in some of these genera several new species were known, but they remain undescribed.
8. Mymaridae. Evidently the only endemic species belong to *Polynema* (widespread), which contains 16 Hawaiian species.
9. Diapriidae. *Phaenopria* has 7 species; *Zacranium* (endemic derivation of *Phaenopria*) is monotypic; *Platymischoides* (endemic, flightless derivative of *Phaenopria*) is monotypic. These are Pacific derivatives.
10. Scelionidae. *Prosanteris* contains 6 endemic species of undetermined affinity. The other genera of Scelionidae evidently all contain foreign species, but *Microphanurus* contains 5 species, some of which may be native, others are known from Fiji.
11. Cynipidae. All of the native species belong to the parasitic Eucoilinae, and although they were split up into several genera, they appear to belong to *Eucoila* with 9 species and *Cothonaspis* with 16 species and 2 varieties. It is possible that these two groups have really descended from one ancestral stock, for there appear to be intermediate species here. A south Pacific derivation of the group is probable.
12. Bethyliidae. *Sclerodermus* has a complex of 16 species; *Sicrola* is the greatest Hawaiian hymenopterous complex with 181 species and 1 variety described. These species have apparently been derived from south Pacific ancestral immigrants.
13. Dryinidae. *Pseudogonatopus* has 2 species which are south Pacific derivatives.
14. Formicidae. All of the endemic ants are of south or western Pacific derivation. *Cerapachys* has 1 species; *Poncra* has 1 species (the others listed in literature have now been found elsewhere). *Pseudocryptopone* has 2 species; *Epitritus* has 1 species. The following genera are represented only by subspecific forms of Pacific species: *Leptogenys* (1 subspecies), *Cardiocondyla* (1 variety), *Strumigenys* (1 variety), *Camponotus* (1 subspecies), and *Paratrechina* (1 subspecies). Some or all of these forms may prove not to be prehistoric Hawaiian endemics. Five of the 15 forms listed as endemics by Wheeler (1934:4) have now been found elsewhere.
15. Vespidae. The Eumeninae are represented by the greatest single complex of the nearly cosmopolitan genus *Odynerus*. There are 104 species and 1 variety endemic. In the closely allied endemic genus *Nesodynerus*

there are 9 species. *Chelodynerus* (monotypic) is an endemic derivation of *Odynerus* as is *Pseudopterocheilus* which contains 3 species. The affinities of the entire group are evidently Oriental, and they appear to represent two ancestral stocks.

16. Sphecidae. The genera *Nesomimesa* and *Deinomimesa*, both endemic and each containing 5 species, appear to have sprung from a single ancestral immigrant *Mimesa*. It has not been ascertained what region is the source of the Hawaiian species. I tentatively refer them to the western sector.
17. Crabronidae. The 22 endemic Crabronidae are placed in five endemic genera as follows: *Xenocrabro* (11 species), *Nesocrabro* (5 species, 1 variety), *Melanocrabro* (2 species), *Hylocrabro* (1 species, 1 variety), and *Orcocrabro* (1 species). All of these species appear to have arisen from a single immigrant ancestor, probably of Asiatic origin.
18. Hylaeidae (Prosopidae). The widespread genus *Hylaeus* (*Prosopis*) is represented by 52 species and 3 varieties placed in the subgenus *Nesoprosopis* erected for them. All of these forms appear to have arisen from a single Asiatic immigrant. Some of the species have independently developed into semi-parasitic forms within the islands.

There are no members of the primitive Hymenoptera of the suborder Chalcidogastera (sawflies, etc.). Only one genus out of the great superfamily of parasites, the Ichneumonidae, is extensively developed in the islands. Excepting the Eupelmidae, the Chalcidoidea is surprisingly weak in endemic forms and many of the species here listed as probably endemic may prove to be immigrants. The Cynipoidea have a fairly well-diversified group of species representing only the parasitic Eucilinae; the gall-formers are unknown here. The ants are poorly represented. The Bethyloidea are represented by the great complex of *Sierola* and a few Dryinidae. The Vespoidea have the extensive development of the *Odynerus* group. The Sphecoidea are represented by the *Mimesa* derivatives and the crabronid complex of genera. The Apoidea has a single extensively developed genus of Hylaeidae. The Chrysidoidea, Scolioidae and Psammocharoidea are unrepresented. The 17 families that are represented in the islands make up only about 16 percent of the families of Hymenoptera. It is significant and noteworthy that the parasitica are conspicuously disharmonic.

XIII. Summary of the Diptera.—There have been nearly 400 named species of Diptera recorded from Hawaii. I have included 246 of these as endemic. The 13 families represented by endemic species make up only about 10 percent of the families of Diptera.

1. Tipulidae. *Limonia* (subgenus *Dicranomyia*) has 12 species, one of which is extraordinary because it is a leaf miner. *Gonomyia* (subgenus *Lipophleps*) has 1 species. The crane fly fauna is typically oceanic. Only the Limoniinae are represented. The large crane flies are absent.
2. Chironomidae. *Chironomus* (well represented in the western Pacific and elsewhere) has 3 endemic species. *Tanytarsus* has 3 endemic species evi-

- dently of south Pacific derivation. Two Samoan species are marine. *Telmatogeton* has 5 endemic species of Pacific derivation. *Dasyhelea* has 1 species evidently allied to south Pacific forms. *Clunio* has 3 endemic marine species of Pacific origin. All of these species, except *Clunio*, are fresh-water aquatics. The extra-Hawaiian species of *Telmatogeton* are marine in habit, and two of these non-endemics are also found in Hawaii.
3. Mycetophilidae. *Platyura* is represented by 3 species, evidently western Pacific derivatives.
 4. Sciaridae. *Sciara* (subgenus *Neosciara*) has 1 species of south Pacific origin.
 5. Dolichopodidae. In numbers of described species, this family leads all others in the native fly fauna. *Chrysotus* has 5 species evidently of western Pacific origin; *Asyndetus* (Pacific) has 1 beach crab-hole species; *Campsicnemus* has 49 species derived from the south or western Pacific; *Emp-peroptera* (endemic, flightless derivatives of some species of native *Campsicnemus*) has 2 species; *Chrysosoma* has 2 species with western Pacific affinities; *Syntormon* has 1 species with western Pacific affinities; *Eurynogaster* (endemic; probably western Pacific in affinity) has 15 species; *Hydrophorus* (widespread) has 2 species which may prove to be immigrants; *Sigmatineurum* (a Pacific derivative) is monotypic and endemic.
 6. Pipunculidae. This family is represented by 12 species of *Pipunculus* leafhopper parasites apparently of south Pacific derivation.
 7. Calliphoridae. *Dyscritomyia* is an endemic genus of 5 species. *Prosthochacta*, closely allied to, if not the same as, *Dyscritomyia*, is endemic and contains 4 species. These flies are the most conspicuous of all of the endemic Diptera. The species whose habits are known have been reared from land shells. The derivation of the group appears not to have been ascertained. They may be allies of *Lucilia*, according to a personal communication from Fritz Van Emden. I tentatively treat them as Pacific derivatives.
 8. Anthomyiidae. *Lispe* has 2 species of south Pacific derivation; *Lispa* has one species with south Pacific affinities; *Lispocephala* has 38 described species, but Perkins (1913:clxxxvii) thinks there are more likely to be nearer 100 species. The Hawaiian species are of south or western Pacific derivation, and the genus appears to be better developed in Hawaii than in any other region.
 9. Sapromyzidae. *Homoneura* has 1 species which may be an immigrant. It has western Pacific affinities.
 10. Trypetidae. *Tephritis* (subgenus *Trypanoidea*) has 5 described species and some known undescribed species of undetermined origin.
 11. Ephydriidae. *Procanace* has 1 species, *Scatella* 6, and *Paralimna* 1 species which may be endemic. These are considered Pacific derivatives. A number of new Hawaiian species await description in this family.

12. Drosophilidae. *Tantalia* is an endemic, monotypic ally of *Drosophila*. *Titanochaeta* is a monotypic, endemic genus of spider egg parasites. *Idiomyia* is an unusual endemic derivative of *Drosophila*; it contains 7 species, among which are the largest of the Hawaiian Drosophilidae. *Drosophila* (widespread) has 47 species and 1 variety (?) endemic, but it has been estimated that there are at least 250 species in the islands. Some of the most remarkable of all *Drosophila* are found in Hawaii, but no study has yet been made of their faunistic affinities. I tentatively place the entire group as Pacific derivatives.
13. Asteiidae. *Asteia* has 2 apparently endemic species with south Pacific affinities. *Bryania* is a monotypic genus now known only from Nihoa. It is an offshoot of *Asteia*.

TABULAR SUMMARY OF THE ENDEMIC HAWAIIAN INSECTS

This summary is a preliminary and tentative attempt to present a very large body of facts in concise form. I am aware that it has many weak points, and that it undoubtedly includes numerous errors. It is too early in our study of the complex Hawaiian fauna to present a more complete and accurate summary, but I believe that this account, weak though it is in many places, is worthy of inclusion here. It may stimulate further research and lead to a more rapid elucidation of the status of some groups than if it were omitted.

The various Pacific, Oriental and Asiatic faunal sectors have been combined for convenience and I have referred to these faunal sources together as "Pacific," to differentiate them from the American. It is sometimes difficult or impossible to assign a descendant line to one sector and exclude another in the Pacific, although some sources are well defined. Details of derivation have been given in the foregoing analysis.

I have combined the subspecific categories under "species" in the table. For convenience, I have totaled the details under each order, and the subtotals are enclosed in parentheses.

The genera have been used as indicators of the sources of the fauna, instead of the species, because I believe that they are more accurate subjects for the purpose. A single introduction may have given rise to over 100 species in one genus, but in another group a lesser number of species may be represented by many genera from many separate introductions.

These totals are not complete and accurate; some of them are only approximations. The totals in columns 6 and 7 refer to the number of genera whose affinities are now known or surmised. Forty-three genera are omitted from these totals because of lack of information. Although these data are admitted to be incomplete and subject to revision, it would take a large shift to alter significantly the conclusions as presented.

SUMMARY OF ENDEMIC HAWAIIAN INSECTS

ORDER	FAMILY	GENERA CONTAINING ENDEMIC SPECIES	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC SPECIES	GENERIC AFFINITIES	
					Pacific	American
THYSANURA	Machilidae	(1)	(0)	(2)	(1)	
ORTHOPTERA	Tettigoniidae	2	2	12	2	
	Gryllidae	4	3	33	4	
	Subtotal (2)	(6)	(5)	(45)	(6)	
CORRODENTIA	Elipsocidae	2	2	10	2	
	Psocidae	1	0	14	1	
	Subtotal (2)	(3)	(2)	(24)	(3)	
MALLOPHAGA	Menoponidae	1	0	3		
	Philopteridae	2	0	2(?)		
	Subtotal (2)	(3)	(0)	(5?)		
ODONATA	Libellulidae	1	1	1	1	
	Aeshnidae	1	0	1		1
	Coenagriidae	1	1	27	1	
	Subtotal (3)	(3)	(2)	(29)	(2)	(1)
THYSANOPTERA	Thripidae	1	0	7(?)	1	
	Phlaeothripidae	4	1	21(?)	3	
	Urothripidae	1	1	1	1	
	Subtotal (3)	(6)	(2)	(29?)	(5)	
HETEROPTERA	Pentatomidae	2	0	15	2	
	Coreidae	1	1	2	1	
	Lygaeidae	11	10	95	11	
	Enicocephalidae	1	0	1	1	
	Reduviidae	1	1	1	1	
	Nabidae	1	0	25	1	
	Anthocoridae	2	1	6	2	
	Miridae	12	9	28	12	
	Saldidae	1	0	4	1	
	Gerridae	1	0	1	1	
	Subtotal (10)	(33)	(22)	(178)	(33)	
HOMOPTERA	Cicadellidae	5	4	73	5	
	Delphacidae	10	8	139	10	
	Cixiidae	2	0	84	2	
	Psyllidae	8	5	31	8	
	Pseudococcidae	6	3	14	6	
	Subtotal (5)	(31)	(20)	(342)	(31)	
NEUROPTERA	Myrmeleontidae	1	0	1	1	
	Chrysopidae	1	1	26	1	
	Hemerobiidae	4	4	27	4	
	Subtotal (3)	(6)	(5)	(54)	(6)	

SUMMARY OF ENDEMIC HAWAIIAN INSECTS—*Continued*

ORDER	FAMILY	GENERA CONTAINING ENDEMIC SPECIES	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC SPECIES	GENERIC AFFINITIES	
					Pacific	American
LEPIDOPTERA	Gelechiidae	2	1	17	2	
	Cryptophasidae	6	6	40	6	
	Cosmopterygidae	14	13	307	14	
	Tineidae	3	1	7	2	
	Yponomeutidae	2	1	7		
	Nepticulidae	1	0	6		
	Batrachedridae	1	0	9	1	
	Caloptilidae	1	0	15	1	
	Bedelliidae	1	0	3	1	
	Orneodidae	1	0	2	1	
	Tortricidae	14	4	70	14	
	Carposinidae	1	0	40	1	
	Crambidae	2	0	7	2	
	Phycitidae	3	2	6	2	
	Pyraustidae	11	5	185	8	2(?)
	Pterophoridae	1	0	5	1	
	Sphingidae	3	1	5		3
	Geometridae	9	4	59	9	
	Phalaenidae	12	2	68	9	2
	Nymphalidae	1	0	1		1
	Lycaenidae	1	0	1	1	
	Subtotal (21)	(90)	(40)	(860)	(75)	(8?)
COLEOPTERA	Carabidae	29	26	222	27	2(?)
	Dytiscidae	2	0	2	2	
	Staphylinidae	12	8	93	12	
	Histeridae	1	0	35	1	
	Nitidulidae	13	12	143	13	
	Cucujidae	2	1	13	2	
	Dermestidae	3	3	20	3	
	Hydrophilidae	1	0	2	1	
	Anobiidae	3	2	156	3	
	Ciidae	2	1	50	2	
	Elateridae	4	3	45	4	
	Eucnemidae	2	1	33	2	
	Alleculidae	2	1	8	2	
	Cerambycidae	8	6	100	2	6
	Anthribidae	1	0	2	1	
	Aglycyderidae	1	0	181	1	
	Curculionidae	14	7	159	12	
	Scolytidae	1	0	23	1	
	Lucanidae	1	0	3	1	
	Subtotal (19)	(102)	(71)	(1,290)	(92)	(8?)

SUMMARY OF ENDEMIC HAWAIIAN INSECTS—*Continued*

ORDER	FAMILY	GENERA CONTAINING ENDEMIC SPECIES	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC SPECIES	GENERIC AFFINITIES	
					Pacific	American
HYMENOPTERA	Ichneumonidae	8	5	40	8	
	Encyrtidae	4	2	24	1	
	Eupelmidae	2	1	57	1	
	Miscogasteridae	5	4	13	5	
	Spalangidae	1	0	2	1	
	Aphelinidae	1	0	2	1	
	Eulophidae	4	0	4		
	Mymaridae	1	0	16		
	Diapriidae	3	2	9	3	
	Scelionidae	2	0	11	1	
	Cynipidae	2	0	27	2	
	Bethylidae	2	0	197	2	
	Dryinidae	2	0	2	2	
	Formicidae	9	0	10	9	
	Vespidae	4	3	117	4	
	Sphecidae	2	2	10	2	
	Crabronidae	5	5	22	5	
	Hylaeidae	1	0	55	1	
	Subtotal (18)	(58)	(24)	(618)	(48)	
DIPTERA	Tipulidae	2	0	13	2	
	Chironomidae	5	0	15	5	
	Mycetophilidae	1	0	3	1	
	Sciaridae	1	0	1	1	
	Dolichopodidae	9	3	78	8	
	Pipunculidae	1	0	12	1	
	Calliphoridae	2	2	9	2	
	Anthomyiidae	3	0	41	3	
	Sapromyzidae	1	0	1	1	
	Trypetidae	1	0	5		
	Ephydridae	3	0	8	3	
	Drosophilidae	4	3	57	4	
	Asteiidae	2	1	3	1	
	Subtotal (13)	(35)	(9)	(246)	(32)	
Grand Total 13 orders	103 families	377 genera containing endemic species	202 endemic genera	3,722 endemic species	334 (95%) with Pacific affinities	17(?) (5%) with American affinities

LIST OF GENERA CONTAINING TEN OR MORE ENDEMIC SPECIES

10-25 SPECIES	26-50 SPECIES	51-100 SPECIES	OVER 100 SPECIES
ORTHOPTERA Paratrigrionidium 16 Banza 11 Leptogryllus 11 CORRODENTIA Psocus 14 THYSANOPTERA Hoplothrips 15 HETEROPTERA Oechalia 15 Oceanides 23 Nysius 24 HOMOPTERA Leialoha 12 Nesothoe 22 NEUROPTERA Nesomicromus 22 LEPIDOPTERA Aristotelia 16 Neclysia 25 Parectopa 15 Eulia 17 Capua 13 Omiodes 23 Pyrausta 11 Orthomecyna 14 Eucymatoge 10 COLEOPTERA Nesocidium 10 Disenochus 13 Atelothrus 20 Mesothriscus 16 Lispinodes 10 Mylaea 11 Gonioryctus 23 Orthostolus 10 Nesopetinus 25 Labrocerus 17 Holcobius 16 Apterocis 14 Acalles 22 Dryophthorus 17 Heteramphus 12 Xyleborus 23 HYMENOPTERA Agrypon 11 Enicospilus 17 Polynema 16 Cothonaspis 18 Sclerodermus 16 Xenocrabro 11 DIPTERA Limonia 12 Eurynogaster 15 Pipunculus 12 Total : 47 genera, 716 species	ODONATA Megalagrion 27 HETEROPTERA Neseis 34 Nabis 25 NEUROPTERA Anomalochrysa 26 LEPIDOPTERA Thyrocopa 34 Aphthonetus 33 Carposina 40 Phlyctaenia 27 Mestolobes 32 Scotorythra 36 Agrotis 29 COLEOPTERA Metromenus 28 Oligota 29 Diestota 29 Acritus 35 Eupetinus 31 Nesopeplus 31 Cis 36 Eopenthes 34 Dromaeolus 32 Neoclytarlus 27 Rhyncogonus 34 DIPTERA Campsicnemus 49 Lispocephala 38 Drosophila 48 Total : 24 genera, 824 species	HOMOPTERA Nesophrosyne 62 Nesosydne 82 Oliarus 79 LEPIDOPTERA Scoparia 64 COLEOPTERA Mecyclothorax 85 Mirotternus 71 Xyletobius 69 Plagithmysus 57 Oodemias 61 HYMENOPTERA Eupelmus 54 Hylaeus 55 Total : 10 genera, 739 species	LEPIDOPTERA Hyposmocoma 216 COLEOPTERA Proterhinus 181 HYMENOPTERA Sierola 182 Odynerus 105 Total : 4 genera, 684 species

THE NUMBER OF ENDEMIC SPECIES PER GENUS

The average number of species per genus for the entire endemic insect fauna is 9.8 (for convenience, I have combined the subspecies and varieties with the species for use in this section). This number is too low, because some of the genera known to have only a single representative in Hawaii may be found to be immigrant, the numbers of species in other genera will be expanded as opportunity arises to describe the new species now at hand and to collect others, and a number of closely allied genera will be combined. In the positively endemic groups, however, the number of forms ranges from 1 to 216 per genus.

The accompanying table includes the genera which contain 10 or more forms.

It is noteworthy that 79.3 percent (2,963) of the endemic species of Hawaiian insects are contained in only 85 genera which include 10 or more species, and 20.7 percent (759) of the endemic species are included in 292 genera, each of which has less than 10 species per genus. The first group contains only positively endemic species, and these average 34 per genus. The second group includes, in addition to unquestioned endemic species, all those species of dubious endemicity and most of the genera which may be merged in the future. The second group has an average of 2.6 species per genus. The first group contains 22.6 percent of the genera containing endemic insects, and the second group contains 77.4 percent. The first group with its large number of species contained in so few genera is a strong index of insularity. Fifty-three percent of the 377 genera which contain the endemic species are endemic.

AN ESTIMATE OF THE NUMBER OF ANCESTRAL SPECIES NECESSARY FOR THE ORIGIN OF THE HAWAIIAN INSECTA

It has long been recognized that the Hawaiian biota has originated from a comparatively small number of immigrants. It is not an easy task to ascertain how many ancestral species gave rise to the Hawaiian insects, but an attempt has been made here which has resulted in some most significant data. There is no doubt that some of these figures will be modified by future research, but it is believed that such revision will not significantly alter the results obtained.

It is estimated that the total number of ancestral species which gave rise to the 3,722 known endemic insects was between about 233 and 254. There is reason to believe that future modification of these last numbers may be downward rather than upward. The significant conclusion reached here is the fact that perhaps only 233 to 254 fertilized female insect immigrants could have given rise to the entire endemic insect fauna! (It will be of interest to note here that only 14 original colonizations have given rise to the entire Hawaiian land-bird fauna.) Of all the data that indicate extreme insularity for the Hawaiian Insecta, these seem to be the most striking. How few have been the successful immigrants over the several millions of years available for dispersal and colonization!

The foregoing figures have been derived from the study of each genus containing Hawaiian insects, but only a summary by order will be given here. In the following list, the first figures refer to the number of ancestral species, and those in parentheses refer to the present number of derived species.

Thysanura	1 (2)	Homoptera	12 to 19 (342)
Orthoptera	3 or 4 (45)	Neuroptera	4 (54)
Corrodentia	2 (24)	Lepidoptera	72 to 73 (860)
Mallophaga	3 to 5 (5)	Coleoptera	39 to 41 (1,290)
Odonata	3 (29)	Hymenoptera	35 to 47 (618)
Thysanoptera	6 (29)	Diptera	31 (246)
Heteroptera	22 to 28 (178)	Total	233 to 254 (3,722)

According to these conclusions, the average number of species derived from each ancestral immigrant has been 14 or 15. These figures are, of course, too low, because the islands have not been completely explored, and the numbers of species in many genera are known to be, or will be found to be, much greater than are now known. The Coleoptera has the greatest average number of derived species, for there are now 31 to 33 species represented for each hypothetical ancestor. The following table shows the approximate average number of derivatives for all of the orders:

Thysanura	2	Heteroptera	6 to 7
Orthoptera	11 to 15	Homoptera	17 to 28
Corrodentia	12	Neuroptera	13
Mallophaga	1 to 2	Lepidoptera	11
Odonata	9	Coleoptera	31 to 33
Thysanoptera	4	Hymenoptera	13 to 17
		Diptera	7

THE HAWAIIAN INSECT FAUNA IS OCEANIC

There is only one possible conclusion to be reached from the study of the foregoing material in regard to the status of the archipelago, and that is that these islands are truly oceanic. There is no evidence whatsoever to indicate that there was any Hawaiian continental land mass or that these islands were ever connected by dry land to any continent. The very character of the fauna expresses the essence of oceanic isolation. How could this impoverished, disharmonic fauna be considered other than extreme in its insularity?

DERIVATION OF THE HAWAIIAN INSECT FAUNA

Although it is admitted that our knowledge is at present incomplete and that numerous errors and irregularities exist in the foregoing analyses, the data displayed by the tabular summary are most significant. There can be no doubt as to the faunistic affinities of the Hawaiian Insecta: they are more than 90 percent Pacific. These conclusions are based upon averages. To attempt to base broad conclusions regarding the derivation and distribution of the biota upon aberrant minorities, instead of the average of the sum of the biota, is to me as

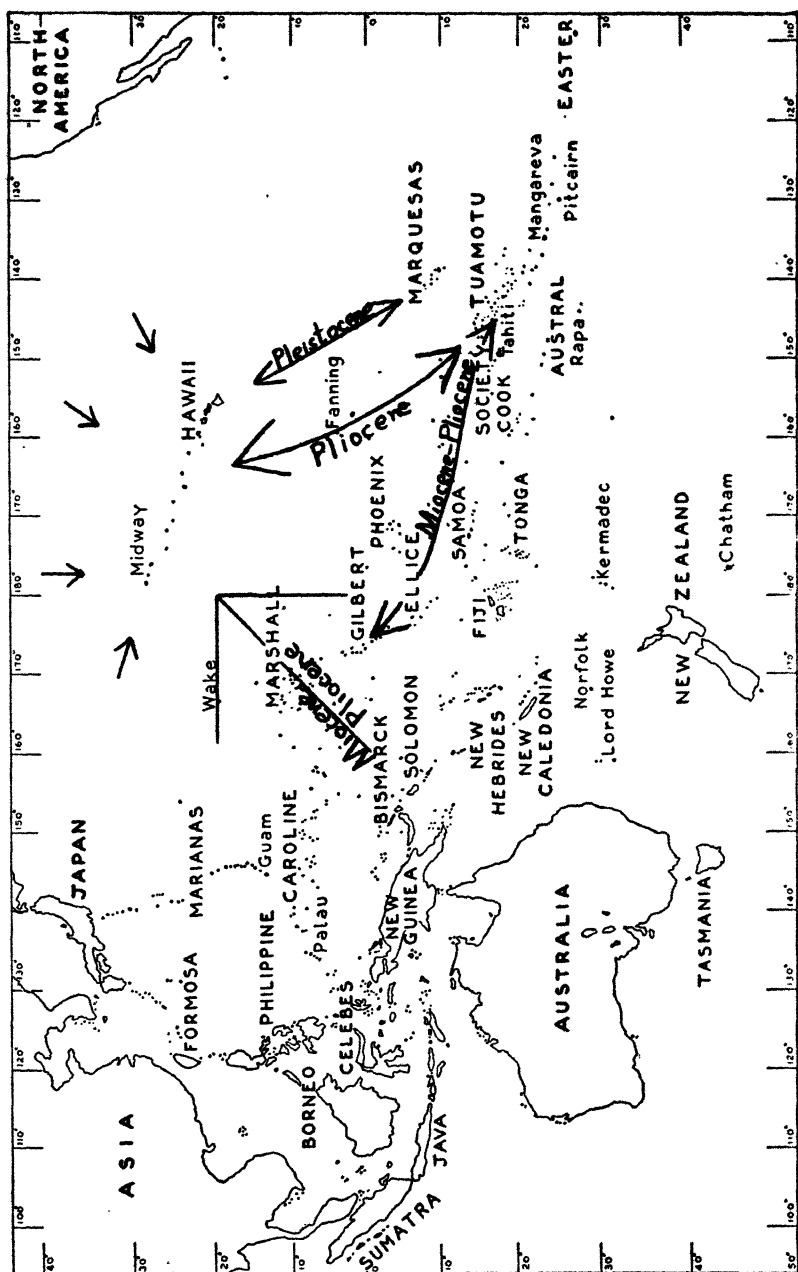


Figure 26.—Hypothetical lines and suggested ages of the principal immigration routes of the endemic terrestrial biota of Hawaii. The Boreal elements are Tertiary to Recent. The eastern Austral routes have continued a limited exchange to the Recent epoch. The southwest sector has long been comparatively inactive.

fallacious as using the extremes of temperature and rainfall, instead of the means, to indicate the temperature or rainfall of a given region. The reason for the weak American representation is the fundamental fact that there has always been an extreme and unbroken water gap of more than 2,000 miles between continental America and Hawaii; whereas, to the south and west there are strings of islands some of which have acted as stepping stones (placed at intervals of at most a few hundred miles instead of thousands of miles) between the Indo-Polynesian regions and Hawaii. Few, indeed, are the insects which have succeeded in crossing the barrier from America. It is noteworthy that most of the American elements are large, strong-flying insects. It should not be overlooked, however, that the continental outlying Aleutian Islands are only about 1,400 miles from the end of the decadent leeward islands (at Kure Island). Also, in future studies we should pay more attention to the past climate of the Aleutians and its bearing upon the flora and fauna.

It is worth while to note here that the endemic Hawaiian plants, in development, endemism and derivation, parallel the insects very closely, for they are considered 92 percent Indo-Pacific derivatives and about 8 percent American and Boreal (see St. John, 1946:378). [But see new data, pages 106-119.] On the other hand, Mayr (1943) has concluded that the birds are predominantly American and Holarctic with only two or three Polynesian lines represented out of 14. The native land snails are about 70 percent Pacific and 30 percent "Holarctic." The Holarctic snail element contains a few recent forms from North America, and one group of over 140 forms in the Cochlicopinae (Leptachatinae) which may be Asiatic in origin, but their source is undetermined.

Insofar as the insects are concerned, it is impossible to divorce Hawaii from the Polynesian Subregion, using that term in its broadest sense. However, there are so many peculiar internal developments that the separation of the Hawaiian Islands into a distinct subdivision is justified. Hawaii has a unique geographical position, and therefore it has a unique flora and fauna for Polynesia. It has received immigrants not only through ancient stepping-stone routes, but also a "rain" of waifs and strays from many points of the compass over a long period of time. It is not as typically Polynesian as Samoa, for example, because it has a large number of non-Polynesian elements overlaying (or underlaying?) its Polynesian base. These elements give it a characteristic facies, and we might refer to the area as the Hawaiian Province of the Polynesian Subregion.

THE NATIVE LAND MOLLUSCA

The endemic Hawaiian land-snail fauna is considered by some workers to be perhaps the most remarkable of all land-snail faunas. The number of endemic genera is proportionately large, and it includes many unusual and isolated types. Because there is no general summary available to use for comparative purposes, I have included a tentative analysis of the group here.

I am indebted to Dr. C. M. Cooke, Jr., and to his protégé Mr. Y. Kondo for

aid in drawing up these notes and supplying much unpublished information from the great and unequaled Polynesian collections at Bishop Museum.

Family HYDROCINIDAE

Three species of *Georissa* (considered a subgenus of *Hydrocena* by Thiele) have been described from Kauai, but, according to Dr. Cooke, they all appear to belong to forms of a single species. These are operculate snails and are probably oviparous. The genus is widespread in tropical and subtropical Europe, Asia and the Pacific. The Hawaiian forms are less than 1 mm. in length and are considered most closely allied to the Tahitian species. The Hawaiian representatives were collected from a clump of moss on a single occasion.

Family HELICINIDAE

These operculate land snails have representatives in many parts of the world, but are evidently absent from Europe, Africa and New Zealand, and are principally a tropical and subtropical group. Most of the Hawaiian species are terrestrial, but a few frequent low shrubs. These are small snails which range from about 3 to 6 mm. in diameter; they are probably oviparous.

Orobophana is distributed from Tonga to the Marquesas in southeastern Polynesia. Seven species and 14 varieties have been described from Hawaii. It is possible that these forms are Hawaiian segregates from *Pleuropoma* instead of representing a distinct stock descendant from the extra-Hawaiian *Orobophana*.

Pleuropoma is distributed from India and Burma to eastern Polynesia. There are 9 species and 29 varieties described from Hawaii.

The 59 Hawaiian members of this family appear to have developed from one, or possibly two, original immigrant stocks.

The two foregoing families are operculates, whereas the following families are all non-operculates and are true pulmonate terrestrial Mollusca.

Family PUPILLIDAE

This family is world-wide in distribution and contains small to minute snails. There is a greater development of species in Hawaii than on any other group of Pacific islands. The Hawaiian species range in length from about 0.75 to 2.5 mm. Most of the Hawaiian pupillids are egg layers, but some are ovoviviparous.

Nesopupa is distributed from Polynesia through the Orient to Africa and St. Helena. In Hawaii there are 20 species, 12 subspecies and 1 variety. Some of these are found on the ground, on rocks and on damp cliffs; one group lives under lichens on tree trunks, and some species are arboreal.

Lyropupa is a peculiar endemic genus which possibly has developed locally as an offshoot of *Nesopupa*. There are 24 species and 12 subspecies, all of which are ground forms.

Pronesopupa contains 10 species and 2 subspecies which evidently have had a local origin from the Hawaiian *Nesopupa*. These species are arboreal.

Pupoidopsis (a close ally of the cosmopolitan *Pupoides*) has a single ground-dwelling representative in Hawaii which appears to be indigenous. The same

species is found on some other eastern Polynesian islands. It appears to be a comparatively recent natural immigrant from America.

Punctum (?) (no anatomical work has been done on our species, and it is not certain that the Hawaiian species belongs to *Punctum*; but the true *Punctum* is widespread) has one ground species (plus other undescribed forms) in Hawaii. The source is undetermined, but it may be North America.

Columella is a Holarctic genus which is also found in the Canary Islands. In Hawaii there are three arboreal species which appear to be American derivatives.

It is possible that four ancestral species gave rise to the 86 Hawaiian forms.

Family COCHLICOPIDAE

The amastrid snails are in a rather confused taxonomic state at present. I follow Watson (1920:24) in placing them as allies of *Cochlicopa*. Cooke and Kondo tell me that there are differences which appear to indicate that *Leptachatina* and its derivatives represent a different line from *Amastra* and its associates. Hence, the two groups are treated here as subfamilies. Pilsbry (1911) and Watson (1920) have found that no apparent differences exist between *Cochlicopa* and *Leptachatina*, but it appears permissible to retain the name *Leptachatina* until further anatomical studies are made.

This group includes the largest of the Hawaiian land molluscs. The species range in size from *Leptachatina*, 6 mm. long, to giant *Carelia*, 85 mm. long. With few exceptions, the species of all genera except *Laminella* are found on the ground; *Laminella* is arboreal.

Subfamily COCHLICOPINAE

The species are all oviparous and all live on the ground.

Leptachatina contains 125 species and 13 varieties and has been found on all of the islands, including fossils on Niihau and Kahoolawe.

Armsia is a local monotypic offshoot of *Leptachatina*, and is found only on Oahu.

Pauahia, a local derivative of *Leptachatina* confined to Oahu, contains 3 species.

One immigrant Holarctic *Cochlicopa* stock could have given rise to these 142 forms.

Subfamily AMASTRINAE

All of the species are ovoviviparous.

Amastra contains 157 species and 68 subspecies contained in several subgenera; with few exceptions, these are all found on the ground.

Laminella has 13 species and 12 subspecies which are arboreal.

Pterodiscus contains 7 species and 2 subspecies all of which are remarkably flattened forms. All of these are ground snails.

Planamastra is an allied group of flattened forms containing 5 species and 1 subspecies.

Carelia is probably the most remarkable of the group, for it includes the giants of the Hawaiian land shells (some are more than 3 inches long). The genus

is restricted to Kauai and its neighboring island of Niihau (fossil only on Niihau). More than one-half of the species are now extinct. Twenty species and 9 subspecies have been described.

It appears that the 294 described forms of this subfamily have been developed from a single basic stock. In spite of the great divergence in the form of the shells, the anatomy shows that all of the genera are closely interrelated.

Family TORNATELLINIDAE

Subfamily TORNATELLININAE

This subfamily is restricted largely to eastern Polynesia, where it has its greatest development and diversity. The classification, however, is in taxonomic chaos. Species have been described from various localities from New Caledonia through Malaya to the Indian Ocean and from Japan, but it has not yet been ascertained whether all of these species belong to the family. A number of extra-Polynesian forms may be found to be synonyms and may be widespread Pacific species; their status remains dubious. The origin of the subfamily is undetermined. The species range in size from about 2 to 10 mm. in length and include both oviparous and ovoviviparous forms.

Auriculella is an endemic genus whose affinities are undetermined. It contains 30 species and 2 subspecies. These forms are arboreal.

Gulickia is an endemic genus containing a single arboreal species which is restricted to West Maui. Dr. Cooke believes that when the soft anatomy is studied the species might be found to be an *Auriculella*.

Elasmias is widespread in the Pacific and it contains three Hawaiian species which are arboreal.

Lamellidea is also widespread in the Pacific and contains 10 species and 3 subspecies, some of which are found on the ground, whereas others are arboreal.

Tornatellides has 46 species and 4 subspecies described from Hawaii, but Dr. Cooke believes that there may be over 100 in his collections. The genus is widespread in the Pacific and contains arboreal and ground species.

Tornatellaria is an endemic genus whose affinities are undetermined, but it appears to be closest to *Tornatellides* and may have developed from that genus. It contains 16 species and 2 subspecies, all found on the ground.

It may be that these 117 forms have been derived from four or fewer ancestral forms.

Subfamily ACHATINELLINAE

This is an endemic subfamily which forms one of the most characteristic elements of the distinctive Hawaiian biota. All of the species are arboreal, and their large size (1 to 2.5 cm.), beautiful colors, striking color patterns and seemingly unending array of varieties have made them the objects of the most intensive collecting and study of any of the Hawaiian molluscs. In appearance they are much like the species of *Partula*. They vie with the drepaniid birds for first place as the most discussed group of the Hawaiian biota, and it was through

his study of these shells that Gulick was inspired to write various articles on evolution, including his book *Evolution, Racial and Habitudinal*.

In spite of all the attention given the group, the origin of the Achatinellinae has long remained obscure. However, its development appears not unlike that of the Amastrinae, and it is now believed by some workers that the group represents only an aberrant local offshoot of the family Tornatellinidae. All the species are ovoviviparous.

No Achatinellinae, living or fossil, are known from the old island of Kauai. Yet, malacologists consider the group one of the oldest of the Hawaiian Mollusca. The Molokai-Maui island complex is suggested as the hypothetical place of origin of the group. From there, the ancestral stock of *Achatinella* (a typical *Partulina* ?) colonized Oahu, where it remained completely isolated for a great length of time. The topographic features of Oahu have been fitted admirably for the breaking up, through geographical isolation, of the mutable *Achatinella* into an astounding number of forms. In comparatively recent geological time, however, *Partulina* has succeeded in recolonizing Oahu—a secondary invasion—but it has not had time to set up a secondary complex. It is interesting that the two other offshoots of *Partulina*, *Perdicella* and *Neacombia*, are found on both Molokai and Maui.

No two authorities seem to be in entire agreement as to what constitutes a genus, species, subspecies, variety or color form in this group. It is truly a complex of complexes. I have followed Caum's list (1928) but have altered it in some places.

Achatinella contains 42 species, 75 subspecies, 4 named varieties and a seemingly unending array of unnamed varieties. The numbers given are tentative and will be subject to change. Welch (1938) added 21 new subspecies to 1 species, and described, but did not name, many new varieties. Gulick, who split the various forms of *Achatinella* finely, said (1905:39), "*Achatinella* is one of ten genera of the Achatinellidae, of which there are between 200 and 300 species and over a thousand varieties, on this island only 40 miles long." This remarkable genus is confined to the island of Oahu.

Partulina is obviously a close ally of *Achatinella*, and it is probably the most primitive genus of the Achatinellidae. Sykes (1900) considered it a subgenus of *Achatinella*, and perhaps its affinities would be better indicated if it were reassigned to that category. Representatives of the genus are found on Molokai, Lanai, Maui and Hawaii with only a couple of species on Oahu. In all, there are 44 species, 28 subspecies and 1 named variety.

Perdicella is an offshoot of *Partulina*. It contains 8 species and 1 named variety and is confined to Molokai and Maui.

Neacombia is another offshoot of *Partulina*. It includes 9 species and 3 subspecies and is confined to Molokai and Maui.

It appears certain that this subfamily had its origin and development in the Hawaiian area and all of the 215 forms listed here may have been derived from a common tornatellinid ancestor.

Family ENDODONTIDAE

This family is world-wide in distribution and many species are found in Polynesia. In Hawaii the genus *Endodonta* has 25 species and 1 subspecies described, but Dr. Cooke believes that the description of material which has come into Bishop Museum in the last 25 years or more will raise the total to more than 100 species. Many of the undescribed species are known only from Recent fossil material collected in the lowlands, where the species have evidently been exterminated.

The Hawaiian species are Pacific derivatives and evidently have arisen from a single ancestral stock with great divergence and development since the original colonization. Some of the species are found on the ground and others live on tree trunks. They range in size from 2 to over 12 mm. and are oviparous. They occur on all the islands.

Family HELICARIONIDAE

This family is world-wide in distribution and is abundantly represented in the Pacific. Some of the Hawaiian species are found on the ground and many are arboreal. The species range in size from about 5 to 13 mm. and are ovoviviparous.

Subfamily EUCONULINAE

This subfamily is represented in Hawaii by 6 species and 2 subspecies of the endemic subgenus *Nesoconulus* of the principally Holarctic genus *Euconulus*. It is noteworthy that the shells of the Hawaiian subgenus and those of a species of the subgenus *Euconulops* from the highlands of Tahiti are larger than those of the continental members of the genus (H. B. Baker, 1938-1941). The eight Hawaiian forms are divided into three taxonomical sections, but may all have arisen from a common Holarctic (Nearctic ?) ancestral stock.

Subfamily MICROCYSTINAE

This is one of the characteristic groups of land snails of Polynesia. The subfamily is "Mainly developed on the islands in the Pacific Ocean but with some species (especially the smaller ones) reaching the East Indies and the mainland of Asia." (H. B. Baker, 1938:10.) According to Baker (1938:11), the subfamily is "closely related to the Euconulinae, which include the most primitive members of the Helicarionidae."

Philonesia is the largest genus of the family found in eastern Oceania, and Baker (1940:106, etc.) has divided it into 13 subgenera, 4 of which are found in Hawaii. The subgenus *Kipua* is confined to Kauai and has 2 species. The subgenus *Waihona* contains 1 species found on the island of Hawaii. *Philonesia*, *sensu stricto*, is, according to Baker's classification, confined to the Hawaiian and Marquesas Islands; in Hawaii there are 24 species and 4 subspecies. The subgenus *Aa* is confined to Hawaii and includes 13 species and 1 subspecies.

Kaala contains a single species and is confined to the higher slopes of Mount Kaala on Oahu. It has characters of both *Philonesia* and *Hiona*.

Hiona is allied to *Philonesia*, is confined to eastern Polynesia and contains 6

subgenera, according to Baker's classification. Two of the subgenera are confined to Hawaii, one is common to Hawaii and the Marquesas and the other three are restricted to southeastern Polynesia. The subgenus *Neutra* has one species on Oahu and one on Uapou in the Marquesas, and each has been placed in a different section of the subgenus by Baker. The subgenus *Hionarion* contains two Kauai species only. *Hiona*, *sensu stricto*, is confined to the Hawaiian Islands and includes 10 species and 3 subspecies found from Kauai to Hawaii.

There are 62 forms contained in the subfamily Microcystinae, and these may have developed from as few as two ancestral stocks.

Family ZONITIDAE

This family is closely allied to the Helicarionidae. Unlike most of the other groups of Hawaiian land snails, all of the Hawaiian representatives of the family are Nearctic or Holarctic derivatives. None of the genera is well developed in the islands, and all of them appear to have become established in the islands in Recent geological time. *Trochomorpha*, so characteristically developed in the south Pacific, has not reached Hawaii. All of the Hawaiian species are terrestrial in habit, and they range in size from approximately 3 to 10 mm. They are ovo-viviparous.

The Vitrininae are represented by a single species of the Nearctic *Vitrina*, found at high altitudes on the island of Hawaii. It may prove not to be specifically different from a northwestern American species. Could it have been carried here by the plover?

The Gastrodontinae are represented by the subgenus *Pseudohyalina* of *Striatura*. *Pseudohyalina* is confined to North America and Hawaii. There are three species in the Territory: one is found on Kauai, and is thought to be the same as a western North American species, and there are two other endemic species.

The Holarctic Zonitinae are represented by three endemic species of the Holarctic and Hawaiian subgenus *Nesozitrea* of *Retinella*, and by three Kauai species belonging to the endemic genus *Godwinia*, which is evidently allied to the American *Patulopsis*.

These 10 species appear to have arisen from four or five comparatively recent immigrants. Because of their habits and habitats, the species which are, or which may prove to be, the same as North American species are considered here to be indigenous rather than artificially imported.

Family SUCCINEIDAE

This family is world-wide in distribution. In Hawaii, the cosmopolitan genus *Succinea* is represented by 44 described species, and the greatest development and diversification of the genus is found in these islands. Many species inhabit other Polynesian high islands. The genus includes both arboreal and ground species; they are oviparous and range in size from 10 to almost 25 mm. Evidently the Hawaiian complex has developed from one ancestral form, but it is not known whence it came. Species of this genus are found on all the main islands.

TABULAR SUMMARY OF THE NATIVE TERRESTRIAL MOLLUSCA

GROUP	GENERA CONTAINING ENDEMICS	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC FORMS	NUMBER OF INDIGENOUS FORMS	AFFINITIES			
					Pacific		Holarctic	
					Genera	Forms	Genera	Forms
HYDROCINIDAE	1		1		1	1		
HELICINIDAE	2		59		2	59		
PUPILLIDAE	6	2	85	1	3	81	3(?)	5
COCHLICOPINAE	3	3	142				3	142
AMASTRINAE	5	5	294		5	294		
TORNATELLINAE	6	3	117		6	117		
ACHATINELLINAE	4	4	215		4	215		
ENDODONTIDAE	1		26		1	26		
EUCONULINAE	1		8				1	8
MICROCYSTINAE	3	1	62		3	62		
ZONITIDAE	4	1	8	2(?)			4	10
SUCCINEIDAE	1		44		1	44		
Total: 10	37	19	1,061	3(?)	26	899	11(?)	161

Fifty-one percent of the genera which contain native land snails are endemic. The average number of native species per genus is 28.8. It is estimated that about 22 or 24 ancestral colonizations gave rise to the 1,064 derived native species. Hence, each postulated ancestor gave rise to an average of from 44 to 48 species. The ancestral amastrid has given rise to the greatest number of derived forms, for there are now 5 genera and 294 known species and lesser forms known in that group.

THE NATIVE LAND AND SHORE BIRDS

The endemic land birds have been so carefully collected that it is extremely unlikely that any living form remains undiscovered. A number of species apparently became extinct in rather recent times without having been collected by scientists, and a deplorable percentage of the described forms is now extinct. So much literature has been assembled on these animals that a detailed summary of them group by group is not needed here. The table on page 105 presents information for comparative purposes.

Sixty-two percent of the genera which contain endemic birds are themselves endemic. The average number of endemic forms per genus is 2.9. Fifteen ancestral immigrants are believed to have given rise to the 70 endemic species and lesser forms. The average number of known forms derived from each of these 15 ancestors has been calculated at 4.6. The ancestral drepaniid gave rise to 42 known forms and is the only line to have speciated extensively in the islands.

The Meliphagidae with its two derived genera and five species is the next important local complex. The Drepaniidae is believed to have been the earliest of this group of organisms successfully to have colonized Hawaii. If the endemic rails are not Pacific derivatives, then 17 percent of the genera and 14 percent of the species are Pacific and 83 percent of the genera and 85 percent of the species are Holarctic. If the rails are Pacific derivatives, then 25 percent of the genera and 18 percent of the species have Pacific affinities and 75 percent of the genera and 81 percent of the species are Holarctic derivatives. (Species and subdivisions of species have been combined under "species" in the foregoing percentages.) There appears to be no doubt that the goose, the hawk, the waterhen, the coot, the stilt and the thrushes are American derivatives. The ducks, the owl and the crow may be either American or Asiatic. The balance of opinion as to the origin of the drepaniids seems to lean more toward America than toward the Palearctic, but much study remains to be done on the group. The sea birds are tropical derivatives and are mostly widespread Polynesian or wider-ranging forms.

TABULAR ANALYSIS OF THE ENDEMIC HAWAIIAN LAND AND SHORE BIRDS

FAMILIA	GENERA CONTAINING ENDEMICS	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC FORMS	NUMBER OF ANCESTRAL STOCKS	AFFINITIES			
					Pacific		Holarctic	
					Genera	Forms	Genera	Forms
ANATIDAE	2	0	3	2			2	3
ACCIPITRIDAE	1	0	1	1			1	1
RALLIDAE	4	1	5	4	2(?)	3(?)	2	2
RECURVIROS- TRIDAE	1	0	1	1			1	1
STRIGIDAE	1	0	1	1			1	1
CORVIDAE	1	0	1	1			1	1
TURDIDAE	1	1	6	1			1	6
SYLVIIDAE	1	1	2	1	1	2		
MUSCICAPIDAE	1	1	3	1	1	3		
DREPANIDAE	9	9	42	1			9	42
MELIPHAGIDAE	2	2	5	1	2	5		
Totals	24	15	70	15	4(6?)	10(13?)	18	57

THE FLORA OF HAWAII

The native plants of Hawaii form an assemblage which has been referred to as one of the most distinctive floras in the world. There are many unusual types represented, such as the shrubby violets, the arborescent lobelias and the peculiar composites. Some of these are old types which correspond to those discussed under the foregoing sections on animals, which appear to be without known living relatives or whose relationships are masked. From these types, there is a gradation down to native forms which are conspecific with species occurring outside Hawaii. These facts duplicate those which have been discussed already for insects, land molluscs and birds.

A section attempting to analyze the flora in accordance with the plan adopted for the insects was started, but I found the problem too involved for anyone other than a skilled botanist with a wide knowledge of Polynesian plants. Therefore, my preliminary manuscript was set aside for about six years, and there was the possibility that this work would be issued without an analysis of the flora. Fortunately, however, F. R. Fosberg, an old friend and a companion of the Mangarevan Expedition, came to Hawaii on a visit when this volume was in press. Dr. Fosberg did not have an opportunity to read the foregoing pages, which were in page proof before his manuscript was received. We were both so busy with other tasks that only a limited amount of time was available for conferences to outline this section. However, in spite of the heavy pressure of other duties and the limited time available, and in spite of the fact that Dr. Fosberg did not have access to his own library or to his invaluable personal notes and manuscripts, he has produced a commendable digest. I am proud and happy to include "Derivation of the Flora of the Hawaiian Islands" as a section of this text, and my indebtedness to Dr. Fosberg is great. We both want to emphasize that this digest, like the foregoing ones, is incomplete and premature, and, perhaps, in part inaccurate, but we believe that such presentations are justified now because they will stimulate further thought and study.

DERIVATION OF THE FLORA OF THE HAWAIIAN ISLANDS

By

F. R. FOSBERG

Speculation as to the affinities and derivation of the Hawaiian flora has not been lacking in the past. Unfortunately there have been more guesses than careful investigation.

The flora is a small one, typically that of an oceanic island. The total known flora of seed plants is, according to the census which follows, 1,729 species and varieties scattered through 216 genera; that of ferns, 168 species and varieties in 37 genera.

Because of its isolation and high endemism, this flora has always attracted attention, and many competent botanists have worked and written on it. It early had one of the finest general descriptive floras (Hillebrand, 1888) ever written on a tropical region. Yet, according to modern standards we know remarkably little about this flora. Many of the most difficult genera have not been monographed. Some monographs which have been written are so poor that they must be redone. The reputation for polymorphism enjoyed by Hawaiian plants has led taxonomists to avoid undertaking major problems on them.

Especially little has been written specifically on the relationships of Hawaiian genera and species to their relatives elsewhere. Even in the most modern and extensive revisions and monographs one frequently finds no indication that the plants have or do not have relatives elsewhere. It seems that much of the work has been done on the assumption that all Hawaiian plants are isolated endemics.

This has made it very difficult to compile any list of the affinities of Hawaiian groups. It has also made the quality of the compilation very uneven. Wherever possible the compiler has relied on his own knowledge or opinions. Unfortunately, there are many groups with which he has had only superficial contact outside of their Hawaiian representation. In the cases of these, an attempt has been made to find where a competent student has expressed an opinion, or to persuade one to express himself. In many instances the last opinion to be expressed was that of Hillebrand 60 years ago. The writings of Dr. Carl Skottsberg have been freely drawn upon. Most of the recent monographs and revisions have given surprisingly little assistance.

It must be emphasized that the present state of our knowledge permits only the most tentative conclusions as to the relationships and origin of most Hawaiian plants, and that even the numbers of species and varieties are by no means definitely known. Current explorations still yield numerous new ones.

Merely writing down some of these approximations may give them more weight than they deserve. However, it has been considered worth while to compile this summary to bring together the best current information.

The tabular arrangement selected, though more complex than that for animal groups, is, if anything, too simple. It seems that the history of plant distribution in the Pacific may have been more complex than that of animals. Plants have

apparently come to Hawaii *from all directions, more or less indiscriminately*, with a preponderance, of course, from the island-rich areas to the southwest. It would be misleading to divide the affinities into Pacific and American, since the Austral group is so strong.

In the tables, where doubt as to two alternatives is expressed by question marks, the least likely of the two has been enclosed in parentheses and the other has been counted in the totaling. In the interest of simplification, question marks have been used only in the most doubtful cases.

The term *Indo-Pacific* is applied to groups following the common distributional pattern of a concentration of species in Indonesia or southeastern Asia and attenuating out into the Pacific, or to groups showing a portion of this distribution: generally, those plants having their affinities to the west and southwest of Hawaii.

Austral is applied to those whose affinities are in the south Pacific, from Australia to Patagonia, but not usually to any extent west of Australia, and not restricted to America. This includes the "Antarctic" element of previous compilers.

American is of obvious circumscription, except that certain plants of far northern connection may be referred to the Boreal category. The Galapagos and Juan Fernandez Islands are regarded as American.

Boreal refers to northern North America and extra-tropical Eurasia. This is not entirely satisfactory, as certain East Asiatic groups should perhaps have a category of their own.

Pantropic includes groups which have such a wide tropical or cosmopolitan distribution that it is difficult or impossible to suggest from which area the original immigrant may have come. A great many of these are groups that are strand or widespread lowland plants.

The *Obscure* category includes such plants as are so isolated as to have no apparent living relatives. There may be some that are placed here only from lack of adequate study. This is certainly true in such ill-classified groups as certain large grass genera, etc. In general, however, these may well be the oldest members of the flora, isolated for so long either that all their relatives have succumbed to competition or to other causes of extinction, or that they have had time to change so completely that evidence of their kinship has been lost.

The philosophy adopted in this tabulation is that actual percentages of the flora are of little significance in speculation on its origin. An attempt has been made to determine by affinities the probable number of original immigrants that established themselves and were the ancestors of the present flora. Countless others may have come, flourished, then become extinct leaving no trace. The indications of the affinities in the tables are on the basis only of these lines of descent. Therefore, the percentages derived from the six general categories of sources do not indicate percentage of the flora but of the original immigrants.

Separate tables have been made for seed plants and Pteridophytes, as their propagules are so different in nature that different principles may well govern their dispersal and distribution. One would naturally expect a much more con-

tinuous rain of microscopic fern spores on an isolated island than of heavy seeds or fruits.

Where genera that are widely accepted are here considered as synonyms (or as subgenera) of others, they are placed beneath the accepted genera in parentheses and in italics. Where several genera are considered to represent the progeny of one introduction, the derived ones are placed in parentheses, but not italicized, under that genus believed closest to the original immigrant. Where there are divergent ideas on the number of species and varieties in a group and the compiler has no definite opinion, the least probable number has been added in parentheses, and this number is not incorporated in the totals. Question marks in the first five data columns indicate strong doubt as to numbers. In the columns under "Affinities" they indicate doubt as to direction of affinity. When alone they are counted as one; when in parentheses they are not counted as they are the less likely alternatives.

Introduced species, either recent or aboriginal, have been excluded where the compiler is satisfied that they are introduced.

SUMMARY OF THE HAWAIIAN SEED PLANTS

FAMILY	GENUS	GENERA ENDEMIC (c); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES				
							Indo-Pacific	Austral	American	Boreal	Pantropic
andanaceae	Freycinetia	w	1	1		1	1				
	Pandanus	w	1		1	1	1				
potamogetonaceae	Potamogeton	w	2		2	2			1		1
	Ruppia	w	1		1	1					1
aiadaceae	Naias	w	1		1	1					1
hydrocharitaceae	Halophila	w	1		1	1	1				
ramineae	Agrostis	w	3	2	1	2		2			
	Andropogon	w	1		1	1	1				
	Calamagrostis	w	2	2		2		2			
	Cenchrus	w	3	3		1	1				
	Deschampsia	w	3	3		1				?	
	Digitaria	w	1		1	1	1				
	Dissochondrus	e	1	1		1			1		
	Eragrostis	w	12	12		2		2			
	Festuca	w	1	1		1				?	
	Garnotia	w	1	1		1	1				
	Heteropogon	w	1		1	1					1
	Isachne	w	2	1	1	2	2				

SUMMARY OF THE HAWAIIAN SEED PLANTS—Continued

FAMILY	GENUS	GENERA ENDEMIC (e) ; NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Cyperaceae	Ischaemum	w	1		1	1		1				
	Lepturus	w	1		1	1	1					
	Microlaena	w	1		1	1	1					
	Oplismenus	w	1		1	1			1			
	Panicum	w	23	23		3			1			2
	Paspalum	w	2		2	2	1				1	
	Poa	w	(3)-4	(3)-4		1			?			
	Sporobolus	w	1		1	1					1	
	Trisetum	w	2	2		1				1		
	Carex	w	9	6	3	6	1	1	2?	1	1	
	Cladium	w	3	2	1	3		2	1			
	(Baumea)											
	(Vincentia)											
	Cyperus	w	23	16	7	8	3		1		4	
	Eleocharis	w	1		1	1		(?)	?			
	Fimbristylis	w	2	1	1	2	1					1
	Gahnia	w	6	6		2	2					
	Oreobolus	w	1	1		1		1				
	Rhynchospora	w	3	1	2	2	2					
	Scirpus	w	(4)-5	1?	4	(4)-5			4		1	
	Scleria	w	1	1?		1			1			
	Uncinia	w	1		1			1				
Palmae	Pritchardia	w	2-(38)	2-(38)		1	1					
Flagellariaceae	Joinvillea	w	1	1			1					
Juncaceae	Luzula	w	3	3		1					1	
Liliaceae	Astelia	w	12	12		1		1				
	Dianella	w	3	3		1	1					
	Dracaena	w	2-(4)	2-(4)		1	1					
	(Pleomele)											
	Smilax	w	2	2		1	1					
Iridaceae	Sisyrinchium	w	1	1		1			1			
Orchidaceae	Anoetochilus	w	2	2		1	1					
	Habenaria	w	1	1		1	1					
	Liparis	w	1	1		1	1					
Piperaceae	Peperomia	w	50	48	2	3	1		1			1
Ulmaceae	Trema	w	1		1	1	1					
Moraceae	Pseudomorus	w	1	1?		1		1				

SUMMARY OF THE HAWAIIAN SEED PLANTS—Continued

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Urticaceae	Boehmeria	w	1	1		1	1					
	Hesperocnide	w	1	1		1			1			
	Neraudia	e	9	9		1						1
	Pilea	w	1		1	1	(?)		(?)		?	
	Pipturus	w	13	13		1	1					
	Touchardia	e	5?	5?		1	1?					
	Urera	w	3	3		2			2			
Santalaceae	Exocarpus	w	3-(5)	3-(5)		1		1				
	Santalum	w	6	6		2		1				1
Loranthaceae	Korthalsella	w	8	6	2	2	1	1				
Polygonaceae	Polygonum	w	1		1	1					1	
	Rumex	w	2	2		1						1
Chenopodiaceae	Chenopodium	w	1	1		1			1			
Amaranthaceae	Achyranthes	w	2	2		1	1					
	Aerva	w	1	1		1	?					
	Amaranthus	w	1	1		1	1					
	Charpentiera	w	3	3		1			1			
	Nototrichium	e	5	5		1			1			
Nyctaginaceae	Boerhavia	w	3		3	3	3					
	Pisonia	w	3	3		2	1	1				
	(Ceodes)											
	(Rockia)											
	(Heimerliodendron)											
Phytolaccaceae	Phytolacca	w	1	1		1			1			
Aizoaceae	Sesuvium	w	1		1	1					1	
Portulacaceae	Portulaca	w	6	4	2	3		1	1		1	
Caryophyllaceae	Sagina	w	1	1		1				?		
	Schiedea	e	45	45		1						1
	(Alsinodendron)											
	Silene	w	5	5		1						1
Ranunculaceae	Ranunculus	w	2	2		1		?				
Menispermaceae	Cocculus	w	1		1?	1		1				
Lauraceae	Cassytha	w	1		1	1					1	
	Cryptocarya	w	2	2		1	1					
Papaveraceae	Argemone	w	1	1		1			1			
Capparidaceae	Capparis	w	1		1	1	1					
	Cleome	w	1	1		1			1			

SUMMARY OF THE HAWAIIAN SEED PLANTS—Continued

FAMILY	GENUS	GENERA ENDEMIC (c) ; NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Cruciferae	Cardamine	w	1	1		1					1	
	Lepidium	w	(3)-4	(3)-4		2	1					1
Droseraceae	Drosera	w	1		1	1				1		
Saxifragaceae	Broussaisia	e	2	2		1	1					
Pittosporaceae	Pittosporum	w	50	50		1	1					
Rosaceae	Acaena	w	2	2		1		1				
	Fragaria	w	1		1	1			1			
	Osteomeles	w	1		1	1	1					
	Rubus	w	2	2		1			1			
Leguminosae	Acacia	w	3	3		1	1					
	Caesalpinia	w	2		2	2					2	
	Canavalia	w	2	2		1	1					
	Cassia	w	1	1		1	1					
	Entada	w	1?		1	1					1	
	Erythrina	w	1	1		1	1					
	Mezoneurum	w	1	1		1	1					
	Mucuna	w	2		2	2					2	
	Sophora	w	1	1		1		1				
	Sesbania	w	1	1		1		?				
	Strongylodon	w	1		1?	1	1					
	Tephrosia	w	1?		1	1	1					
	Vicia	w	1	1		1			?			
	Vigna	w	3	2	1	2					1	1
Geraniaceae	Geranium	w	6	6		1	1					1
Zygophyllaceae	Tribulus	w	1		1	1					1	
Rutaceae	Fagara	w	14	14		1	1					
	Pelea	w	94	94		1	1					
	(Platydesma)	e										
Euphorbiaceae	Antidesma	w	6	6		1	1					
	Claoxylon	w	8	8		1	1					
	Drypetes	w	1	1		1	1					
	Euphorbia	w	60	60		1	1					
	Phyllanthus	w	2	2		1	1					
Aquifoliaceae	Ilex	w	1		1	1		1				
Celastraceae	Perrottetia	w	1	1		1	?					
Anacardiaceae	Rhus	w	1	1		1	1					

SUMMARY OF THE HAWAIIAN SEED PLANTS—Continued

FAMILY	GENUS	GENERA ENDEMIC (e) ; NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Sapindaceae	Alectryon	w	1	1		1	1					
	Dodonaea	w	18	18?		1					1	
	Sapindus	w	2	2		2	1		1?			
Rhamnaceae	Alphitonia	w	1	1		1	1					
	Colubrina	w	2	1	1	2	1?				1	
	Gouania	w	3	3		1	1					
Tiliaceae	Elaeocarpus	w	1	1		1	1					
Malvaceae	Abutilon	w	3	2	1	2			1			1
	(<i>Abortopetalum</i>)											
	Gossypium	w	1	1		1			?			
	Hibiscadelphus	e	4	4		1						1
	Hibiscus	w	10	9	1?	4	2?	1			1	
	Kokia	e	4	4		1						1
	Sida	w	2		2	2	1				1	
Sterculiaceae	Waltheria	w	1	1		1			?			
Theaceae	Eurya	w	2	2		1	1					
Violaceae	Isodendron	e	4	4		1			?			
	Viola	w	7	7		1						1
Thymeleaceae	Wikstroemia	w	14	14		1	1					
Flacourtiaceae	Xylosma	w	2	2		1	1					
Cucurbitaceae	Sicyos	w	8	8		1						1
Myrtaceae	Eugenia	w	4	4		2	2					
	Metrosideros	w	18?	18?		1		1				
Begoniaceae	Hillebrandia	e	1	1		1						1
Halorrhagaceae	Gunnera	w	7	7		1			1			
Araliaceae	Cheirodendron	w	5?	5?		1		1				
	Reynoldsia	w	1	1		1		1				
	Tetraplasandra	e	10?	10?		1						1
	(<i>Picrotropia</i>)											
Umbelliferae	Daucus	w	1		1	1			1			
	Hydrocotyle	w	1		1	1					1	
	Peucedanum	w	3	3		1						1
	Sanicula	w	4	4		1						1
	Spermolepis	w	1	1		1			1			
Ericaceae	Vaccinium	w	8	8		1		1				
Epacridaceae	Styphelia	w	2	1	1	1		1				

SUMMARY OF THE HAWAIIAN SEED PLANTS—Continued

FAMILY	GENUS	GENERA ENDEMIC (e) ; NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Primulaceae	Lysimachia	w	13	12	1	2	1	1?				
Myrsinaceae	Embelia	w	2	2		1	1					
	Myrsine	w	25	25		1?					1	
Sapotaceae	Nesoluma	w	1		1	1		1				
	Pouteria (Planchonella)	w	6?	6?		1	1					
Ebenaceae	Diospyros (Maba)	w	7	7		1	1					
Plumbaginaceae	Plumbago	w	1		1	1	1					
Loganiaceae	Labordia	e	75	75		2	2					
Gentianaceae	Centaurium	w	1		1	1			1			
Oleaceae	Osmanthus	w	1	1		1	1					
Apocynaceae	Alyxia	w	1	1		1	1					
	Ochrosia	w	1	1		1	1					
	Pteralyxia	e	2	2		1						1
	Rauvolfia	w	7	7		1						1
Convolvulaceae	Breweria	w	2	2		1						1
	Cressa	w	1		1	1			1			
	Cuscuta	w	2	2		1			1			
	Ipomoea	w	9	4	5	7	5				2	
	Jacquemontia	w	1	1		1			1			
Hydrophyllaceae	Nama	w	2	2		1			1			
Boraginaceae	Heliotropium	w	2	1	1	2		(?)	2			
Verbenaceae	Vitex	w	1		1	1	1					
Labiatae	Lepechinia	w	1		1	1			1			
	Phyllostegia	w	108	108		1		1				
	(Stenogyne)	e										
	(Haplostachys)	e										
	Plectranthus	w	1		1	1	1					
Solanaceae	Lycium	w	1		1	1			1			
	Nothoecstrum	e	6	6		1			1			
	Solanum	w	7	7		1						1
Scrophulariaceae	Bacopa	w	1		1	1					1	
Myoporaceae	Myoporum	w	1	1		1	1					

SUMMARY OF THE HAWAIIAN SEED PLANTS—Continued

FAMILY	GENUS	GENERA ENDEMIC (e) : NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Gesneriaceae	Cyrtandra	w	110	110		1?	1					
Plantaginaceae	Plantago	w	19	19		2?		2				
Rubiaceae	Bobea	e	4?	4?		1	1					
	Canthium	w	1		1	1	1					
	Coprosma	w	27	27		3?		3				
	Gardenia	w	2	2		2	2					
	Hedyotis	w	76	76		1	1					
	(Gouldia)	e										
	Morinda	w	3	3		1	1					
	Nertera	w	1		1	1		1				
	Psychotria	w	11	10	1	2	1		1			
	(Straussia)											
Campanulaceae	Brighamia	e	2	2		1						1
	Clermontia	e	42	42		1		1				
	Cyanea	e	100	100		1						1
	(Rollandia)	e										
	(Delissea)	e										
	Lobelia	w	23	23		1	?					
Goodeniaceae	(Trematolobelia)	e										
	Scaevola	w	12	11	1	1	1					
Compositae	Adenostemma	w	1		1	1	1					
	Argyroxiphium	e	61	61		1						1
	(Wilkesia)											
	(Dubautia)	e										
	(Raillardia)											
	Artemisia	w	5	5		1				1		
	Aster	w	1	1		1			1			
	Bidens	w	60	60		1		1				
	Gnaphalium	w	1	1		1					1	
	Hesperomannia	e	7	7		1			1			
	Lagenophora	w	3	3		1		1				
	Lipochaeta	e?	55	55		1	1					
	Remya	e	2	2		1			?			
	Tetramolopium	w	20	20		1	1					
Totals 83	216	28e 188w	1,729	1,633	96	272	109	45	50	7	35	28

The table of seed plants yields the following information:

- 83 families
- 216 genera
 - 28; 13 percent endemic
 - 188; 87 percent non-endemic
- 1,729 species and varieties
 - 94.4 percent endemic
 - 5.6 percent non-endemic
- 272 original immigrants
 - 40.1 percent Indo-Pacific
 - 16.5 percent Austral
 - 18.3 percent American
 - 2.6 percent Boreal
 - 12.5 percent Pantropic and Cosmopolitan
 - 10.3 percent Obscure

Significantly absent are gymnosperms, *Ficus*, Cunoniaceae, mangroves, *Piper*, Bignoniaceae, Araceae, and the several large predominantly American tropical families. Significantly few are Orchidaceae, palms, Loranthaceae, Lauraceae, Scrophulariaceae. Significantly numerous are grasses and Compositae.

Not evident from the table is the interesting fact that of the American element a far greater part of the species are only slightly distinct from their American relatives (probably indicating geologically recent arrival) than is true for the other elements.

For the Pteridophyte table much of the basic information was kindly supplied by W. H. Wagner, Jr. However, the generic concepts, arrangement of the table and interpretations are those of the compiler.

The Pteridophyte table shows that there are:

- 10 families
- 37 genera
 - 3; 8.1 percent endemic
 - 34; 91.9 percent non-endemic
- 168 species and varieties
 - 119; 64.9 percent endemic
 - 49; 35.1 percent non-endemic
- 135 original immigrants
 - 48.1 percent Indo-Pacific
 - 3.7 percent Austral
 - 11.9 percent American
 - 4.4 percent Boreal
 - 20.8 percent Pantropic and Cosmopolitan
 - 11.1 percent Obscure

Most notably absent are *Cyathea* (sensu lata) and *Blechnum*. (*Sadleria*, however, is of blechnoid affinity.)

SUMMARY OF THE HAWAIIAN PTERIDOPHYTES

FAMILY	GENUS	GENERA ENDEMIC (e) ; NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Psilotaceae	Psilotum	w	2	1	1	1					1	
Lycopodiaceae	Lycopodium	w	13	9	4	9	4		1		4	
Selaginellaceae	Selaginella	w	3	3		3				1	1	1
Ophioglossaceae	Ophioglossum	w	4	1	3	3	1				2	
	Botrychium	w	1	1		1	1					
Marattiaceae	Marattia	w	1	1		1	?		(?)			
Schizaeaceae	Schizaea	w	1	1		1		1				
Gleicheniaceae	Gleichenia (sensu lata)	w	4	2	2	3	2		1			
Hymenophyllaceae	Hymenophyllum (sensu lata)	w	3	3		3	1				2	
	Trichomanes (sensu lata)	w	6	5	1	6	3	2			1	
Polypodiaceae	Adiantum	w	2(?)		2(?)	2(?)	1(?)				1	
	Asplenium (sensu lata)	w	21	12	9	21	13		2	2	2	2
	Athyrium (Diplazium)	w	9	7	2	9	6		2			1
	Cibotium	w	5	5		1	?		(?)			
	Coniogramme	w	1	1		1	1					
	Cystopteris	w	1	1		1					1	
	Diellia	e	8	8		1						1
	Doodia	w	2		2	2		2				
	Doryopteris	w	2	2		1					1	
	Dryopteris (Lastrea) (Ctenitis) (Cyclosorus)	w	25	20	5	25	14		5		2	4
	Elaphoglossum	w		9		9	5				2	2
	Histiopteris	w	1		1	1					1	
	Hypolepis	w	1		1	1	1					
	Lindsaea	w	1		1	1	1					
	Microlepia	w	2		2	2	2					
	Nephrolepis	w	4		4	4					4	
	Pellaea	w	1		1	1			1			

SUMMARY OF THE HAWAIIAN PTERIDOPHYTES—Continued

FAMILY	GENUS	GENERA ENDEMIC (e) ; NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES						
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure	
Marsileaceae	Polypodium (<i>Pleopeltis</i>) (<i>Microsorium</i>) (<i>Grammitis</i>) (<i>Xiphopteris</i>) (<i>Amphoracnium</i>)	w	16	13	3	7	3		1	2		1	
	Polystichum (<i>Rumohra</i>) (<i>Cyrtomium</i>) (<i>Phanerophlebia</i>)	w	4	2	2	4	1		1	1		1	
	Pteridium	w	1	1		1			1				
	Pteris	w	4	3	1	3	1				2		
	Sadleria	e	(4)-5	(4)-5		1						1	
	Schizostege	e	1	1		1						1	
	Sphenomeris	w	1		1	1	1						
	Tectaria	w	1	1		1					1		
	Vittaria	w	1		1	1	1						
	Marsilea	w	1	1		1			1				
	Totals 10	37	3e 34w	168	119	49	135	65	5	16	6	28	15

The low percentage of Austral affinities is interesting in view of Dr. Copeland's (1939) derivation of almost all ferns from Antarctica, and in view of the much higher percentage in seed plants. Interesting, also, is the relatively low endemism and, particularly, the low ratio (1.24) of present species and varieties to original introductions.

Tables for the lower cryptogams were not prepared because of the lack of critical knowledge of these groups on the part of the compiler, and also because of the rudimentary state of available information on Hawaiian members of many groups.

These statistics from the two tables clearly support the commonly held idea that the flora is basically an attenuated Indo-Malayan one, but not nearly so predominantly so as previously thought. The American element, on the present basis, is stronger than the most commonly accepted recent view has held.

The picture, on the basis of the small number of original immigrants, the diversity of their origin and the important groups not represented, seems to be that of a flora that has always been insular. It is exactly the type that might be expected to be descended from a random aggregation of chance waifs carried overseas by a combination of factors such as storms, currents and birds. Of seed plants, an average of one successful arrival and establishment every 20,000 to 30,000 years would account for the flora. This is granting an estimate of 5 to 10 million years of above-water history for the entire Hawaiian chain, starting with the islands at the extreme northwest, such as Kure, Midway and Lisianski.

The preponderance of Indo-Pacific affinities seems satisfactorily explained by the number of islands in that direction as compared with the lack of islands to the east and north. The Austral element, too, is more or less in proportion on this basis.

If we resort to land bridges or continents to account for the presence of the Hawaiian flora, then we may well have to build them in all directions.

CHAPTER 4

DEVELOPMENT OF THE ENDEMIC FAUNA

Although I appreciate and admire the vast amount of experimental zoology that has been done within recent time, yet, when it is all considered, it does not give direct or indirect evidence enough to base a belief in evolution upon. This belief is based upon nature's own experiments, upon our studies of development, comparative morphology and anatomy of living and fossil animals, upon the geographic distribution in past and present time, and the time sequence as shown by fossils. Most of this information is the direct result of systematic zoology. . . . Yet we are constantly being told that systematic work is only worthy of inferior intellects, and that great intellects turn their attention to . . . other superior subjects.

—Muir (1924:480)

It has been shown that upon these oceanic islands of Hawaii there has been developed an array of endemic organisms characterized by certain features which mark the Hawaiian biota as one of the most distinct in the world. The extreme isolation of the archipelago has resulted in great restriction upon the types of organisms which have succeeded in reaching it and becoming established. We have estimated the number of ancestral immigrants and have found that only a relatively few individuals have given rise to the extensively developed groups of genera and species now existing here. It now follows that some discussion of evolution and the nature of the development of the biota should be included.

The contemporary endemic floras and faunas of the Hawaiian Islands are largely those which have developed upon lands which, for the most part, we can examine today. A fundamental problem is, therefore, an analysis of these floras and these faunas upon *this* land. It is not so much a question of the foreign ancestors of the contemporary biota as it is a study of the biota as it exists today. The rate of erosion is such that these main islands could not have stood here as they are longer than from a period late in the Tertiary. An attempt to place the main islands farther back in the geological time scale would be unsupported by geological facts. We are dealing with many specific complexes of plants and animals which owe their very existence to the developments which have taken place on visible insular landscapes or on those which can be reconstructed by the interpretation of erosional and topographic features. If it is admitted that geographical isolation is a factor in evolution, and that geographical and topographical barriers are of fundamental importance, then it must be admitted that such evolution as has taken place on a given island has come about through the interplay of influences which may have been brought about on the land upon which the organisms exist today. Moreover, the lesser phylogenetic categories, as well as some of the higher categories, resulting from such evolution must be

admitted to be younger than some of the topography. We speak of "explosive" speciation resulting in the large complexes of species so common in the islands. I believe that these outbursts of species development have resulted in part from the late Pliocene and particularly the great Pleistocene erosion which has left such a spectacular and rugged topography in its wake. *New land open to colonization is conducive to speciation.*

INTER-INSULAR SEGREGATES AND EVOLUTION

One of the most commonly discussed features of the Hawaiian biota is the extreme isolation of certain of its components. There are a number of genera whose relationships appear to be so cryptic that no one has yet been able to discover anything closely allied to them outside of Hawaii. Various explanations are given to account for these phenomena, including the commonly expressed theory calling for a great, ancient, foundered continent, land area or bridge.

Various factors or combinations of factors have influenced the biota to produce these special results, and no one explanation can account for all of them. From my studies of island life, I have been led to conclusions which, it appears to me, may shed some light upon the intricate and perplexing problem. At the beginning, each of these islands was barren of life—each a sterile mound of steaming lava surrounded by ocean (fig. 7); so we must look elsewhere for the source of the original immigrant stocks. But where should we turn to discover the ancestral affinities of these many groups of organisms which are peculiar isolates, whose relationships are most cryptic and whose allies are masked or have been lost from the residuum of the evolution of Pacific biotas?

To account for some of the aberrant Hawaiian segregates, the following explanation is proposed. All of the Pacific island insect faunas which I have studied have their own characteristic developments. Thus, in the large weevil genus *Microcryptorhynchus* (more than 100 species described and many undescribed), which is distributed through most of the south Pacific from Australia eastward to the Marquesas and to western Micronesia in the north Pacific, most islands or island groups have characteristic divergent species or groups of species. For example, the only known species with well-developed sclerotic spines or tubercles at the bases of the elytra are found on Guam; the only smooth, shiny, black species are found on Rapa. Such great structural deviations are found among species of the Society and Austral Islands that a person unfamiliar with the group would be likely to place various species in different new genera, and some are so distinct that they might be placed in different tribes or even different subfamilies! As a matter of fact, some of these allied species will run to different subfamilies in existing keys in use in other parts of the world. These various species have developed and diverged in their isolation upon their respective islands. If one of these highly divergent species should happen to be carried by some agent of dispersal to another island and be successful in establishing itself, the new population set up might, given ample time and complete isolation, develop an entirely new group of divergent species, many of which might be utterly different

from the basic stock that gave rise to the species on the ancestral island. If one of the more divergent species of the second population series is in turn isolated on another island, the process will repeat itself and the intensity of divergence will be increased. Now, if enough time has elapsed, the original island sources will have passed through a period of intense erosion and may perhaps be reduced to atolls, their characteristic faunas will have been exterminated and out on the newer island will be left peculiar segregates without obvious ancestral relationships. This theory may be elucidated by the diagram included as figure 27.

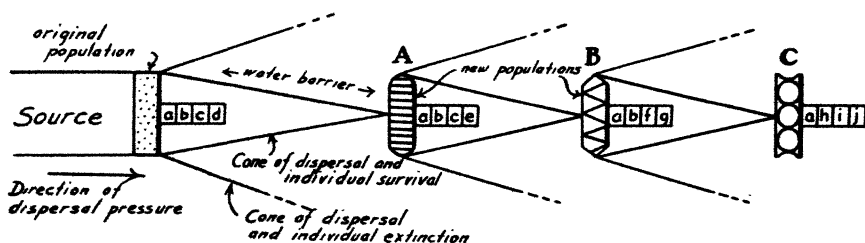


Figure 27.—A diagram to illustrate the theory of inter-insular segregate evolution as explained in the accompanying text.

A, B and C each indicate an archipelago. The lower-case letters in the squares indicate hypothetical characters of an organism, and the changes in letters indicate evolution and the divergent immigrant stocks which have populated A, B and C. According to Darlington's formula (1938:274), if the distance between Source and A, and between A and B are the same, and the chance of survival of an individual from Source to A is 1 out of each 1,000 dispersed, then the chance of an individual from Source reaching B is only 1 in 1,000,000 (compare fig. 28).

The diversity of the fauna, as based upon *suprageneric categories*, will be inversely proportional to the distance between Source and A, B or C. The greater the distance between any of these points, the more disharmonic will be the out-

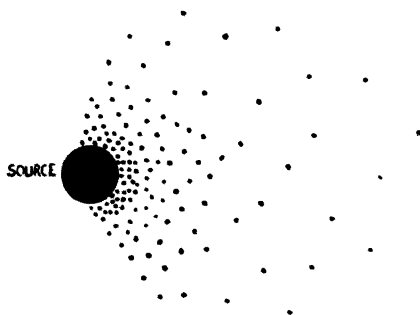


Figure 28.—A diagram to illustrate dispersal intensity. The opportunity of an island lying to the right of Source to be colonized by overseas dispersal is inversely proportional to the distance between it and Source.

lying biotas. The greater the age and isolation of C, the greater will be the percentage of endemism and the greater will be the peculiar forms of life. If A and B archipelagos are eroded away, and their terrestrial biotas thus exterminated, it may be difficult or impossible to reconcile various elements of C with Source. Thus, Hawaii appears to be in the position of C, with A and B now represented by coralline archipelagos. Time and extreme isolation are essential for the development of a biota such as that of Hawaii. One of the reasons why the Hawaiian biota is so unique and has so many endemic forms is because of its great isolation which was especially emphasized when some of the ancient routes of immigration were eliminated by the formation of atolls.

One of the most significant points to keep in mind here is the lifting out of a population (and quite possibly an aberrant population) a single fertilized individual from which may spring a new and isolated population series and eventually an array of forms. The impregnated female carries only the genotypes of herself and her mate, not the genetic make-up of an inbreeding species population. She does not represent an average of her population. The implications and potentialities of such action are great.



Figure 29.—Radiation within a single group of Hawaiian land snails. This plate shows the comparative sizes and shapes of 11 groups of Amastrinae. The snails in the top row, left to right, are: *Laminella gravida* (Ferrusac), *Amastra* (*Paramastra*) *turritella* (Ferrusac), *Amastra* (*Metamastra*) *textilis* (Ferrusac), *Amastra* (*Cyclamastra*) *sphaerica* (Pease), *Pterodiscus wesleyi* (Sykes), *Planamastra digniphora* (Ancey). Bottom row, left to right: *Carelia turricula* (Mighels), *Amastra* (*Amastra*) *violacea* (Newcomb), *Amastra* (*Armiella*) *knudseni* (Baldwin), *Amastra* (*Kauaia*) *kauaiensis* (Newcomb). All figures are natural size. According to the thesis developed here, it is believed that any one of these snails might set up an entirely new evolutionary line, if through the natural processes of the development of oceanic faunas it were introduced into a new area and succeeded in establishing a new population. If, for example, the extremes of *Carelia* and *Planamastra* were removed to new archipelagos of high islands with unfilled, favorable ecological niches and given time, is it not easily understood how they might set up such distinctive lines of radiating types that they would ultimately end in complexes equivalent to what we find today in the drepaniid birds and similar well-known developments? (I am indebted to Dr. Cooke for helping me to arrange this plate.)

We should not lose sight of the fact that every individual of a population differs in a number of ways (gene differences). Any change in the gene complex of an organism is reflected upon the other genes of that organism, and once a change is made it is believed that other changes may follow in a more or less geometric increase with consequent accelerating action on further change and ultimately on species formation. If this action be accompanied by conditions conducive to isolation and survival, then rapid and diversified speciation may follow. Islands are ideal places for such processes. We may have introductions, reverse introductions back to the original source and reintroduction upon reintroduction after time-lapses sufficient to change the original populations as well as the new (fig. 45). This may be repeated over and over again with consequent formation of large species complexes. This method is not restricted to inter-island segregation, but it may apply to mountains and ranges, to ridges and valleys, to dry and wet areas, to highlands and lowlands, to hostplants, and, in the case of sedentary land snails, perhaps even to different rock piles or to isolated trees.

A fundamental, inescapable fact is that we are dealing here with *small* populations—often unusually small populations. It is these small populations which restrict gene flow and encourage random divergence where nonadaptive characters can flourish, and these populations exist in an environment favorable to the survival of changed or changing forms. The loss of the power of flight in one of these populations, even if drastic and rapid, need not be detrimental to the changed population, for if that population is situated in a favorable niche, it may continue to thrive because in this particular instance the power of flight would not be vital to existence.

The isolated products of such inter-insular segregate evolution may lead some workers to the conclusion that a given present-day biota is of great age, whereas actually the contemporary biota may be in comparative youth and its distinctiveness is but a reflection of its mode of origin and development. Thus, to me the Hawaiian biota, although it is truly an old insular one, appears not to belong to geological antiquity.

This biota of Hawaii is "older than the rocks"—in a way. One of the most significant features of the development of our flora and fauna appears to have been overlooked in previous discussions. Those who have argued for great age for the main Hawaiian Islands (an age far beyond what geological facts allow for them), to account for the ultimate development of the biota, have advanced the opinion that this biota has developed entirely upon these present main islands or upon a hypothetical continental mass of which they are the remnants. This opinion is, in my considered judgment, a fundamental error. The biota as we know it today is in part the ultimate product of a progressional development which has moved and evolved along great insular archipelagos over periods of time much longer than the ages required for the development of the main Hawaiian Islands and their contemporary biota. Various genera and stem forms of groups of species may have evolved in islands—now atolls such as some of the leeward Hawaiian chain, the great Micronesian archipelagos, the Line Islands—which form the

approaches to Hawaii. However, some of the genera and the bulk of the species known today have originated on our present main islands. This is obvious from their developments, distribution and interrelationships. Some have come directly from North America or elsewhere. The crux of this argument is that in contemporary Hawaii there are preserved remnants of a biota which has in part developed by unique methods and in which are preserved forms which are the end products of species chains that carry back, through archipelagos now worn away, to geological ages indeterminate.

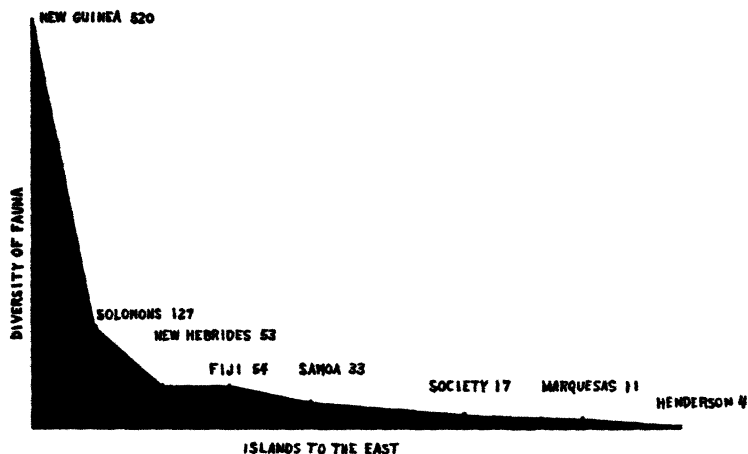


Figure 30.—A typical curve of progressive insular biotal deficiency in the Pacific. This chart shows the number of native land birds in several south Pacific archipelagos from New Guinea eastward. These data (from Mayr, 1940) are nearly complete. Similar curves can be drawn for most groups of organisms in the area.

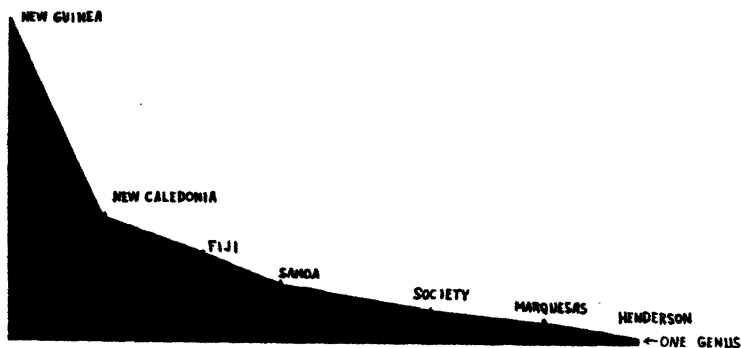


Figure 31.—A curve of progressive insular biotal deficiency derived from a group of insects for comparison with the preceding curve of bird distribution. This curve has been derived from an analysis of the genera of the weevil subfamily Cryptorhynchinae. The data from Samoa westward are incomplete and unsatisfactory, and the curve will rise much more abruptly on the west when our collections from the area are reported upon.

I believe that the great atoll chains of the Pacific may hold some of the now hidden clues to the stories of the magnificent biological development of Polynesia. Many of the peculiar endemic groups of the Hawaiian and southeastern Polynesian islands owe their existence, if not their very origin, to ancient high islands of the one-time splendid archipelagos now marked by clusters of coral reefs. Surviving lines of middle Tertiary and of perhaps even older continental faunas may have had their germ plasm filtered down through succeeding changing generations which have passed successfully through island maturity and degradation to atoll formation and have carried over to new high islands in different archipelagos. Thus, some supposedly old types such as certain land molluscs could have maintained themselves (but evolving) in insular isolation through long periods of time while their continental progenitors became extinct or restricted under continental conditions. Thus, for groups like the Aglycyderidae (Proterhinidae) with representatives on certain Atlantic and Pacific islands only, and for such isolated snails as the Tornatellinidae, we find a possible explanation for most peculiar types of distribution and development. Atolls have been overlooked, generally, because most of them are so alike floristically, faunistically and in outward physiographical appearance, because they are more or less biological deserts terrestrially and because they contain few or no endemics to excite the biologist looking for *new species*.

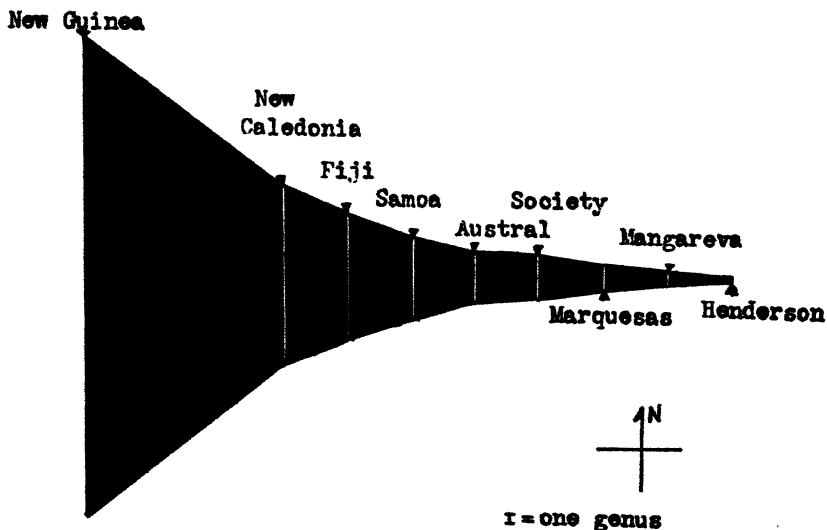


Figure 32.—A diagram based upon the same data as the preceding curve. If one turns the chart on its side so that the point is downward, it will appear as a great funnel fitted with graded filters, and one can visualize the ocean barriers between the islands acting as finer and finer sieves which progressively exclude more and more genera as one progresses from west to east. This chart is based upon several hundred species included in more than 100 genera.

GEOGRAPHICAL METAMORPHOSIS AND EVOLUTION

By their very nature, mid-Pacific high islands have comparatively fast-changing topographies. Speed of erosion is great, and the results achieved are remarkable. The comparative influence of topographic change upon the biota is not specifically known, but from the resulting patterns of evolution in the biota, it appears that the effect is great. Within confined land areas, the principle outlined in the discussion of inter-insular segregates and evolution may be applied to a lesser degree. When it is discovered that on one side of a river there are certain organisms which are different from allied forms on the other side of the river, it appears obvious that the river may have had some influence on the distribution and evolution of the respective forms. The same applies to mountain ranges, ridges and valleys. Moreover, if such barriers have acted upon or resulted in the differentiation that is observed, then the evolutionary products must be younger than the topographical features which exerted the pressure.

There is an old statement which is brought up whenever we speak of Hawaii in terms of geological youth. It is: "If you say that these islands are of late Tertiary age, then the fauna is older than the rocks!" To a degree, that is correct, for, if looked upon in a particular way, part of the fauna is older than these rocks. Is not the fauna of certain glaciated areas, in the sense of the land being capable of supporting a flora and fauna, essentially older than the newly uncovered land left after the retreat of the glaciers? Of course it is; and now in such areas there are groups of organisms which are known to be of pre-Glacial age—some of them are archaic—and which have maintained their lines elsewhere during glaciation. But, we can compare only some of the higher categories here in Hawaii. Because, if it is admitted that isolation is a major factor in evolution, then the species, and even some of the higher categories, must be acknowledged as being developed upon this land, and it must be admitted that such forms are younger than the rocks. To account for some of the supra-specific developments in Hawaii, reference can again be made to the chart and discussion of inter-insular segregates in the foregoing section (fig. 27). By such selection, isolation, development and extinction, it is considered that higher categories such as those represented in the Hawaiian biota may be accounted for. However, this theory is not proposed as a "cure-all," because there are many other factors at work now and others which may be recognized at some future time which must also be taken into consideration. But it is believed that this interpretation, or modifications of it, will be useful in aiding in the analysis of some of the peculiar developments of Hawaii.

It is considered probable that some of our unusual endemic genera were well differentiated in the Hawaiian area before the present main islands rose from the sea. An early development in the leeward Hawaiian islands when they were high and forested, and the subsequent passage of certain elements from those early faunas and floras to the new eastern islands as the western islands eroded down, are considered most possible.

Far to the south of Tahiti lies the unique, greatly eroded, isolated island of Rapa, and almost 50 miles to the east of it is situated a group of about ten almost

unknown rocks called Marotiri or Bass Rocks. Most of these rocks are awash, but four of them rise precipitously to elevations estimated to be between 200 and 300 feet (quite similar in appearance to illustrations in figures 23 and 24). These rocks appear to be all that is left of an ancient island, probably similar to Rapa, which has been almost completely eroded away. All the exposed rocks serve as nesting places for myriads of sea birds, and the deposits of excrement and bird remains are thick. However, we found there a dozen species of plants, some of them distinct new species, and on some of those plants were found new species of insects and spiders. The insects belong to genera which are characteristic of the well-watered forests of high islands. I consider these species to be the last survivors of a fauna which had its beginning upon the slopes of a high, densely forested island, and believe these few forms, now eking out a most precarious existence and at the point of extermination, to be among the only species which were adaptable and fortunate enough to continue their populations through the very drastic changes brought about by the tremendous erosion, degradation and

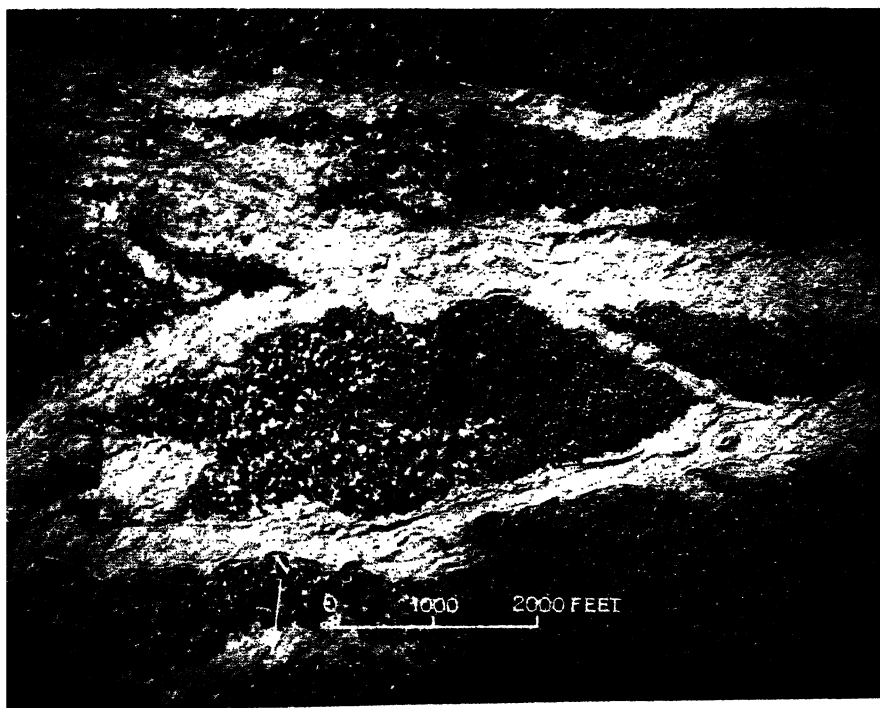


Figure 33.—A vertical air view of aa lava flows of 1916 and 1926, at an altitude of 4,000 feet on the southwest slope of Mauna Loa, to show appearance in a forest with an annual rainfall of about 50 inches. The gray color is caused by a complete cover of lichens. Note the "kipukas," or islands of forest cut off and surrounded by the lava flows. Compare the following figure. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)

partial submergence of their environment. At least some of these Marotiri species stand by themselves in their genera. The dispersal of one of such peculiar species to a new and favorable locality may result in the development of a distinctive set of species which might in time be called a section of a genus or, in more time, a higher category. Marotiri cannot last much longer, for it has almost entirely returned to the sea, and soon all of its original terrestrial biota will be lost forever. Could not part of the unique biota that is found on Rapa today have had its origin on ancient Marotiri?

In these islands of Hawaii, built by successive lava flows and pyroclastic ejectamenta, the upbuilding process may in itself have exerted an influence upon evolution by isolation and extermination. A visit to the island of Hawaii, for example, where volcanic activity is at present continuing, will reveal "islands" of climax forest ranging from a few acres to many square miles in extent surrounded by great areas of barren lava flow "deserts" (figs. 33, 34). These "islands" are termed "kipuka" (key-poo-kah) by the Hawaiians. Within the kipukas are found plants

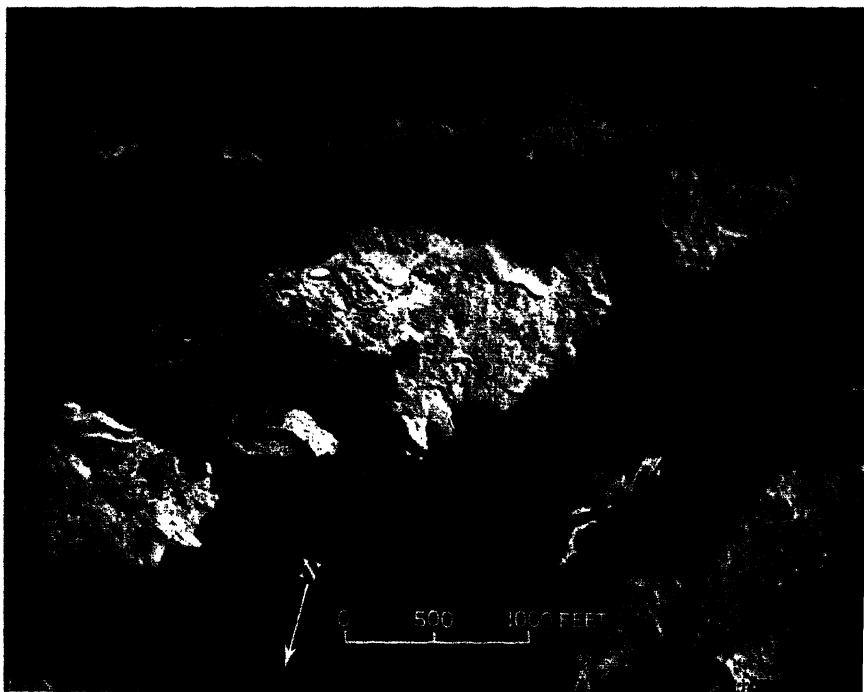


Figure 34.—A vertical air view of bare black aa lava flows of 1916 and 1926 at an altitude of 6,500 feet, six miles northeast of those shown in the previous figure and above the forest, where the rainfall is about 30 inches annually. Compare the previous figure, and note the contrast in the vegetation of the lava flows because of the differences in rainfall. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)

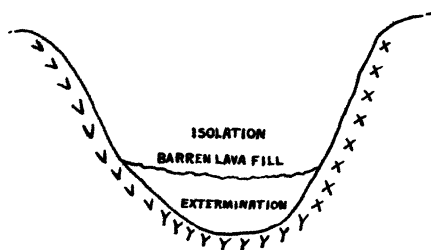


Figure 35.—Diagram showing how isolation may be achieved by recurrent volcanism filling the floor of an old valley with lava. The V, Y and X marks along the valley margins represent a population which is distributed in a linear manner along the mountain range and differs in some characters from right to left. It is presumed that the ancestral population spread into the area from the right.

and animals which have been cut off from the surrounding areas by the fiery rivers of lava which have killed and buried all living things in the area over which they have passed. The flows break up populations into series of small populations,

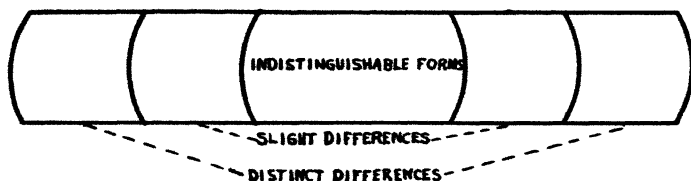


Figure 36.—A diagram of a "species chain." The vertical lines might represent ridges separating valleys including the major populations.

sometimes over wide areas, and the long, bare, inhospitable flows form, for a time, barriers to population movement. Within one of these kipukas Rock found some trees which have been found only in a 56-acre "oasis." In this same kipuka the only known surviving individual of the remarkable tree *Hibiscadelphus giffardianus* was found. This endemic genus is evidently an offshoot of endemic species of *Hibiscus*, and three species from Hawaii and one from Maui have been discovered. Rock considered that the plant association found in the kipuka represented the type of forest which extended over a considerable area before most of it was wiped out by lava flows. Future lava flows may result in the extermination of

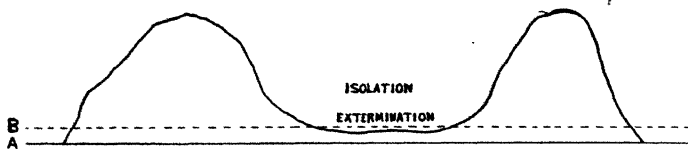


Figure 37.—Diagram showing how isolation of faunas of two mountain ranges may be achieved by a rise in the level of the sea. A, old level; B, new level.

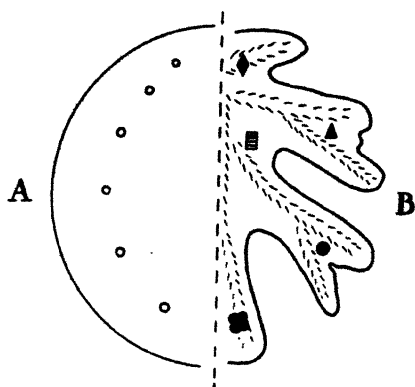


Figure 38.—A diagram illustrating changes brought about on an island through age, erosion and the subsequent isolation of changing populations on the dissected and rugged topography of the areas longest exposed to erosion. **A**, indicates a relatively new island area with little erosion and a species widespread over it. **B**, represents the area after a lapse of time sufficient to develop a rugged topography of deep valleys and high, steep ridges with derived, changed populations representing new evolved entities inhabiting isolated areas and/or different ecological situations made available by erosion, but not available on the new area at **A**.

some contemporary species. Giffard (1925:146), speaking of the *Oliarus* leafhoppers, said, "The maculate Kilauea examples of *inconstans*, with one exception, were taken by the author from mixed scrubby vegetation in an old crack or fissure in the arid desert hardly a stone's throw from the edge of the Halemaumau active crater. (This deep fissure was later filled up by the 1922 lava flow.)" The breadth of the lava flows varies considerably, but some of them are one to several miles across, as much as 10- to 30-feet thick and many miles long. Some few kinds of plants are quick to become established on new flows in areas of abundant rainfall, but it takes years for the forest to come back on the flows and develop a climax association once again. The rate of reforestation is, of course, dependent upon the locality, elevation and rainfall (figs. 33, 34).

If extensive volcanism recurred on a well-eroded island, the resultant filling of valleys and older surfaces would, if extensive enough, leave large areas of barren lava fields separating small "islands" of forest and could conceivably wipe out many species and subspecific forms and leave small isolated populations to persist in widely separated areas. The subsequent expansion and development of these species populations might be somewhat akin in character to the overseas dispersal heretofore discussed. If the forms of a single species were disposed in a linear manner along a mountain range, as A B C D E, and recurrent volcanism completely covered B, C and D, leaving A and E as distinct and isolated populations with the intermediate forms wiped out, we might have distinct species. Other workers have pointed out that the terminal forms of some species chains act as distinct species, but that through allied links in the chain, the two ends may be traced together by backtracking (fig. 36).

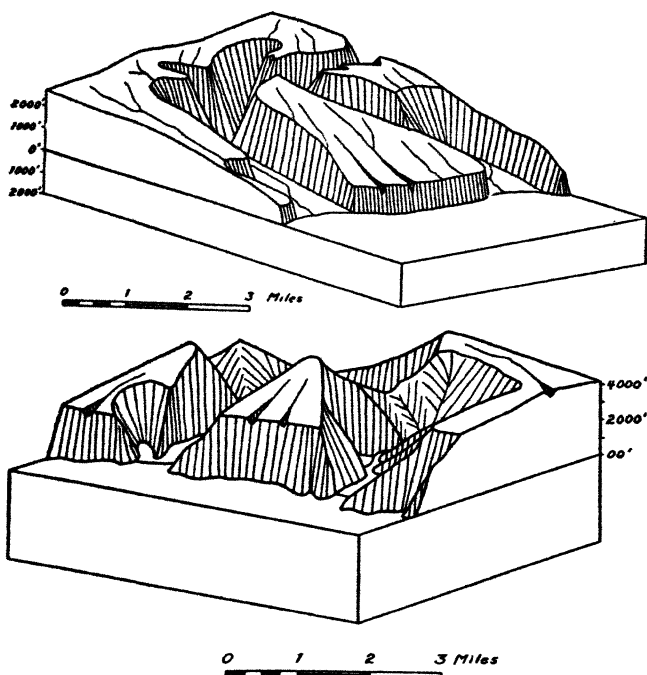


Figure 39.—Block diagrams illustrating erosional patterns in deeply dissected Hawaiian areas. These diagrams illustrate well the profound erosion and stream piracy which have left facet-like remnants of the original cone surfaces isolated by great cliffs and deep valleys. They illustrate also how populations of plants and animals may be isolated by the rapid erosion characteristic of the regions. Note that the facets consist of areas of only slightly altered sections of the original flow slopes of the volcanic mass. The top figure is of Waipio and Waimanu Valleys on Hawaii. The lower figure is of the Pelekunu-Wailau section of Molokai. (After Wentworth, 1928.)

On geologically Recent island areas, such as parts of the great island of Hawaii, many organisms, some birds excepted, have a particularly wide range. However, on the older island areas many species tend to have a much more restricted range. Also, the number of species, and especially divergent or very distinctive forms, are greater on the older areas. It appears that the break-up of some species goes hand in hand with the changes of topography brought about by intense erosion.

We may diagram this viewpoint as shown in figure 38. "A" represents a new, comparatively slightly eroded surface, with a species widespread over it. "B" represents the area after long erosion has cut it up into great ridges and deep valleys which contain isolated, different kinds of derived organisms.

It appears that some species may become widespread on a newly available area; then, because of inherent plasticity or other causes, they divide up into a number of forms which become further modified and isolated until new species are formed.

The rugged topography of our islands is conducive to such speciation. Some of our puzzling, complex species of Hawaii appear to be such forms. At every opportunity new forms appear to be established, and these intra-insular segregates are common in Hawaii.

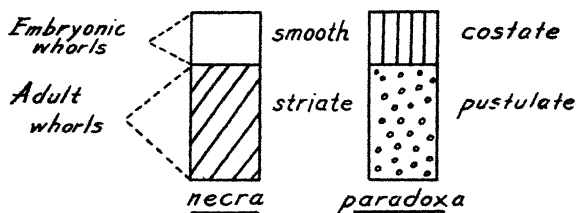


Figure 40.—The characters of *Carelia* used in the accompanying text diagrammed.

When we go into Hawaiian mountains in search of particular kinds of organisms, unless they be common, widespread species, we do not just go into the mountains anywhere. We select certain mountains, certain ridges, certain valleys or particular small areas at specified elevations and exposures in such regions. We know by experience that a given species found on one ridge will not be found on the next ridge across a certain deep valley. In other words, extensive field work has shown that many organisms are remarkably limited in their distribution to small areas in Hawaii. Some forms of Hawaiian land snails can only be found in localities which are to be measured not in square miles but in square yards. If a few species of land snails are brought to the Bishop Museum from a restricted area—from one clump of trees and ferns, for example—it is possible to tell the collector where the specimens came from, not only as to island or mountain range, but definite information on the elevation, side of valley or ridge and the character of the environment at the particular spot where the specimens were collected can be supplied! In some groups it is also possible for the specialist to predict where a certain species may be found when the only specimens known are the types which lack locality data. We take risky excursions to outlandish places because we know that in uniquely isolated, difficult-to-get-to localities we are likely to find peculiar new species. This all leads to the conclusion that, no matter how they act, topographic and geographic isolation do have decided evolutionary significance.

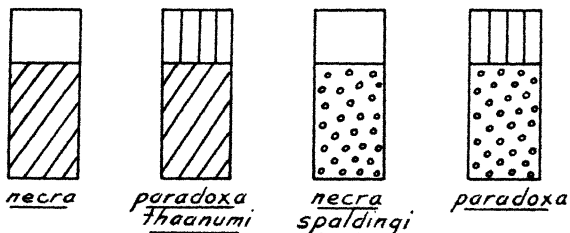


Figure 41.—Diagrams of the characters of *Carelia* and hybrids as explained in the text.

The Carelia paradoxa Land-Snail Complex.—On the eastern side of Kauai, at and near the mouth of the Wailua River, four kinds of *Carelia* snails have been found in Recent fossil beds. These four forms present a most interesting problem which has been outlined to me by Dr. Cooke. The four forms are *Carelia paradoxa*, *Carelia paradoxa thaanumi*, *Carelia necra* and *Carelia necra spaldingi*. The forms *thaanumi* and *spaldingi* have been called subspecies. The two species, *paradoxa* and *necra*, are separated from each other by the Wailua River. However, the subspecies are each found across the river from the typical forms. Thus, *paradoxa* and *necra spaldingi* are found on the north side, whereas *necra* and *paradoxa thaanumi* are found on the south side. The peculiar thing is not so much the distribution of the shells as it is their puzzling morphological characters. *C. paradoxa* has costate embryonic whorls and pustulate adult whorls. *C. necra* has nearly smooth embryonic whorls and striate adult whorls. These are represented diagrammatically in figure 40.

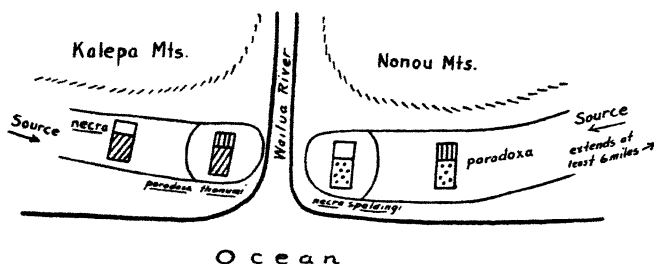


Figure 42.—The distribution of *Carelia paradoxa* and *Carelia necra* and their supposed hybrid forms.

These "subspecies" appear to be hybrids. Their morphological features are peculiar because *necra spaldingi* has the embryonic whorls of *necra* and the adult whorls of *paradoxa*; *paradoxa thaanumi* has the embryonic whorls of *paradoxa* and the adult whorls of *necra*. These four forms are diagrammed in figure 41 and a diagrammatical representation of the distribution of these molluscs is shown in figure 42.

It is noteworthy that the characters of the embryonic whorls, which are considered basic and most important for use in tracing phylogenetic relationships, are carried

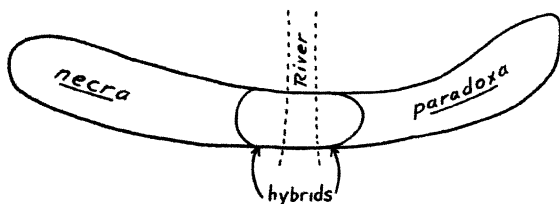


Figure 43.—A diagram to illustrate an alternate explanation of the development of the supposed hybrid populations of *Carelia necra* and *Carelia paradoxa*.

across, whereas the particular adult characters are found on one side of the stream only. Why should not some *paradoxa thaanumi* be found with *neera spaldingi* and vice versa?

There are two explanations for the distribution of these apparent hybrid populations. One is that the species approached the river and some individuals from both sides crossed the stream and mixed with the opposite species. The other explanation is that there appears to be reason for believing that the river once flowed southward (left on the diagram, figure 42) around the Kalepa Mountains and the two species met on undivided ground; then the stream cut through the mountains and separated the zone of hybrids as indicated in figure 43.

Unfortunately, these *Carelia*, and most of the other members of the peculiar genus, are now extinct or apparently extinct, and it is impossible to make as detailed a study of such interesting problems as is desired. There are only certain places where conditions favorable for the preservation of these dead shells obtain. These are in dunes and in sandy areas. Fossil shells do not last long in pure lateritic soil, and where there is no calcareous sand to preserve them, they ordinarily cannot now be found. Therefore, the distributions which I have indicated in the diagrams are partially diagrammatic reconstructions. The *paradoxa* group is considered the most specialized of *Carelia* as based upon the study of the embryos. About 1,000 specimens of the group were examined by Dr. Cooke.

Segregation of Lymnaea Snails in Different Streams on Kauai.—Dr. Cooke has supplied some notes which are recorded here as a most interesting case of segregation. A species of fresh-water snail (*Lymnaea*) was found to have both sinistral and

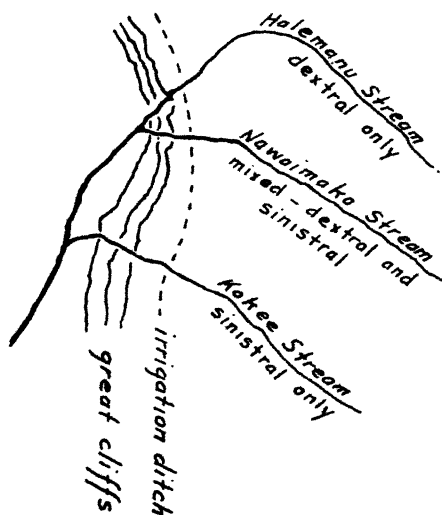


Figure 44.—A diagram to illustrate the distribution and segregation of *Lymnaea* snails in different streams on Kauai.

dextral shells in Nawaimaka Stream, but in the next stream to the south (Kokee) all shells collected were sinistral, and in the next stream to the north (Halemanu) all snails collected were dextral. These streams tumble over a cliff which is about a thousand feet high and then merge in valleys below. Unfortunately, the canyon area below the cliffs has not been adequately explored by shell collectors; it is difficult of access. An irrigation intake ditch has been built above the cliffs and taps each of the three streams mentioned. The most recent collections of snails from the streams show that the artificial breaking of the barriers between the streams has resulted in the mixing of shell types near the irrigation ditch in each of the three streams. It is assumed that the mixing up of shell types will gradually proceed headward until all of the streams are completely occupied by mixed shells. The diagram shown in figure 44 illustrates the problem.

SOME OTHER FACTORS OF SPECIATION

Single rules cannot be made to blanket all evolution. Each particular case must be considered as a separate problem. After proper study of each unit, the grouping of particular kinds or degrees may be made. It cannot be said, for example, that because host isolation has acted in the formation of some species it is the rule that must be laid down for all species. There is no reason why we should consider just one or a few methods as essential to the origin of species. What has taken place in some land snails with their sedentary habits may not be exactly the same in every instance as that which has taken place in volant organisms.

Speciation tends to be held within certain bounds, and it is only occasionally that great breaks occur which set up exaggerated species groups, new genera and the like. The all-important factor is whether or not a new type can survive and reproduce population continua which in turn specifically diverge to form species complexes. There are evidently certain limits of divergence outside of which it appears difficult to go and beyond which success is seldom achieved.

The more we study evolution, the more evident it appears that there are various ways by which new forms arise. We cannot hope to cover all phases of the problem here, but we should call attention to some examples which appear relevant.

There are two fundamentals which have to do with the origins of species upon these islands. One is isolation; the other is small populations. Most of our insular populations are small. Frequently, colonies of only a few individuals are the rule. Isolation is of various kinds and grades, but geographical and host isolation appear to be the types which are the most active or at least the most apparent causative factors here.

The environment, of course, plays an all-important part in the development of species, but there is more than one side to the question. It is generally agreed that profound changes have been effected on organisms by environment. There appears to be another factor involved here, too. From what I have seen in the Pacific, certain organisms appear to have selected certain environmental conditions, rather than being what they are as the result of environmental influence. For example,

certain mutant forms which have arisen from causes other than environmental may search out niches best suited to them, and they adopt an environmental category.

One of the principal reasons why there are so many species in Hawaii is the division of the area into several large islands. If the main Hawaiian islands were a single land mass, I believe that species development would not have been what it is today. The division of the group has resulted in the duplication of species. What is now a group of six species which has evolved because of isolation, on each island from Kauai to Hawaii, might be only a single, wide-ranging species if continuous land were available.

The nature of the growth of the islands was, similarly, conducive to the multiplication of species. For example, the two mountain ranges of Oahu were at one time two islands separated by a narrow water barrier. We now find species on one range whose ancestors arose in the opposite range, apparently when the two ranges were separate islands. The faunas of the two areas are distinct, although they are now connected by dry land. The old elements are most distinct; some of the newer ones blend or cross from one range to the other. Molokai, Maui and Hawaii have had similar developments.

The old elements of Maui, Molokai and Lanai are quite distinct, one from the other. The channels between these islands are so shallow that geologists say that the three islands were connected by dry land not so long ago. This is reflected in the insects, because there are a number of forms which hardly differ on these three islands and many species are common to all. In fact, when discussing some groups, we may assemble the species of Molokai, Maui and Lanai and consider them as occupying a single island.

The separation of the islands brings into play the principles of invasion and re-invasion, (fig. 45). Much of the speciation which has taken place appears to have been the result of single individuals having been removed from one island and

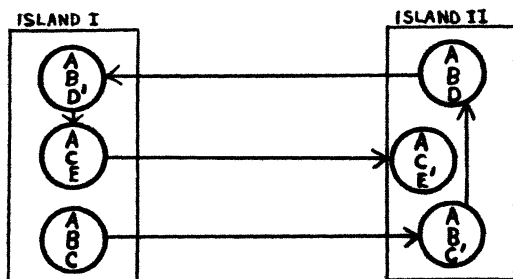


Figure 45.—A diagram illustrating the principles of invasion and re-invasion. The circles represent species, the enclosed letters, their characters. If a single gravid individual of population ABC becomes established on island II, that individual and the new population it gives rise to will not represent the average of all of the characters of population ABC: hence it is represented by ABC' on island II. A lapse of time and continued isolation of the ABC' population may give rise to form ABD. If ABD in turn invades island I, it may be so evolved as not to mingle with ABC, its original ancestral stock, and island I will have two distinct forms. This process may repeat itself many times over if conditions are favorable, and, of course, if long intervals of time are involved.

carried across an ocean barrier to another island where a new population was set up. This factor is of utmost importance. The new colony, beginning from one or a few individuals completely isolated from the parent stock, will early display certain differences. The new stock will have part of the characteristics and hereditary units of its ancestral population, but not all of them, and it is not an average of the base stock. It will be different from the average from the very beginning. This changing population might be swamped out if further invasion is made soon from its parent population. However, it may remain isolated for long periods of time, because of the infrequency of successful over-water dispersal. The longer it remains isolated, the more distinct it will become. In time, the new population will be so changed in character that even if another invasion is made by the parent stock, it will remain separate because it has become a distinct species. Over long periods of time, a series of invasions from island "A" to island "B" may be made. If these are made at sufficiently long intervals, then each invasion may set up a distinct species. After island "B" is colonized, the new changed populations may reverse the invasion route and return to the home island "A," where they would maintain themselves as distinct species which would in turn develop into distinct forms. Each of these new populations will, of course, come under the influence of local conditions and may diverge into additional species within each island.

The Hawaiian goose is, geologically, relatively a newcomer to Hawaii, but it remained isolated for so long after its ancestral *Branta* from North America colonized the islands that it developed a distinct form. It is already a widely differentiated goose which in form and habit is so distinct from its forebears that some ornithologists have placed it in a distinct genus.

The giant Hawaiian dragonfly, *Anax strenuus* Hagen, is an endemic offshoot of the wide-ranging Boreal *Anax junius* (Drury). A colony of *A. junius* was established in Hawaii long ago, and this colony remained isolated until it had diverged so much from typical *A. junius* that now it can be called a distinct species, as it really is. More recently *A. junius* has re-invaded Hawaii and succeeded in again becoming established. We now have these two closely allied forms living side-by-side but remaining quite distinct. As a matter of fact, the two forms are known to attempt copulation, but no hybrids are known to have developed, and the populations remain quite distinct and are differentiated easily. The endemic species tends to be more of a mountain species, whereas the later comer, *A. junius*, is mostly a lowland form which only rarely extends its range into the mountains. Perhaps when the islands were wooded to the shore line, the endemic *A. strenuus* was more widespread but adapted to a forest life, and as the lowland forests receded the dragonfly retreated with them. Dean Amadon has called my attention to the fact that the *Phacornis* thrushes have invaded Kauai twice. An early invasion of Kauai followed by a long interval of time has resulted in the development there of a distinct full species, *P. palmieri*. At a more recent date, *P. obscura*, a species with subspecies on Hawaii, Lanai, Molokai and Oahu, found its way to Kauai and is now represented there by a subspecies.

It appears that most of the endemic groups have established themselves in Hawaii by a single chance invasion. However, there are certain groups which appear to have arisen from two or more invasions. One of these is the *Odynerus* wasp complex. Two lines appear to be represented here: an ancient one composed of about 100 species and a much more recent one represented by *O. nigripennis* and its three allies. The Hawaiian *Nysius* bugs appear to have developed from several invasions.

The developments within the islands reflect clearly the differences in the breadths of the channels separating them and hence the ease or difficulty of over-water colonization. Data on the breadths of the channels are given on page 7. It has been pointed out that some of the groups on the closely associated islands of Maui, Lanai and Molokai (Kahoolawe is included in this assemblage but its endemic biota is unknown because of early extermination) showed close interrelationships. The greatest over-water gap between the main islands is that between Oahu and Kauai (about 75 miles). A more isolated island may be expected to have a more distinctive fauna because it is less exposed to "pollution" by repetition of immigration. Kauai is richly endowed with well-marked and distinctive forms. In many groups, the species found on Kauai are the most divergent. Some birds which have subspecific forms on the other islands have clear-cut species on Kauai. All the *Odynerus* wasps of Kauai are endemic to Kauai, but all the other main islands have an overlapping of species. Some species of bees which are found on several of the other islands are replaced on Kauai by distinct species. A factor which also is involved here is that Kauai is considered the oldest, or one of the oldest areas, of the main islands. Certainly its greater age is reflected in its biota, but its greater isolation also has played a dominant role in its local developments.

Perkins (1913:xl) noted that:

The extreme sluggishness of so many of the insects and mollusca leading to great restriction of locality, which we observe also in the birds must lead to extreme inbreeding. We have observed colonies of some of the flightless beetles to persist for years on a single tree and where these colonies are isolated from others, no doubt all the inhabitants have resulted from a few stray examples, probably often from one. While the food supply remains in suitable condition these isolated colonies thrive and become very numerous, but they are, doubtless, often totally exterminated when it becomes no longer suitable, unless, by chance, individuals can reach some other tree fit to supply a breeding ground. Obviously this sluggishness and restriction of range must itself diminish the numbers of individuals of a species, and the tendency of island creatures to limit their range and to specialize their habits is a striking feature of the fauna.

We might expect the loss of flight in a group to make it more subject to easy isolation and hence more liable to speciation. However, the presence or absence of wings cannot be correlated with rate of evolution. Of the four genera of insects in Hawaii containing over 100 species, *Proterhinus* with 181 forms is flightless, *Odynerus* with 105 is fully winged as are *Sierola* with 182 and *Hypsoecoma* with 216. Only 2 out of 14 genera containing 50 or more species are flightless.

One of the most wonderful fields of study in Hawaii is the hostplant relationships

of the insects. The evolutionary role played by hostplants is a major and fundamental one. Usinger, in concluding his *Nysius* monograph (1942:162), said:

The conclusion seems inevitable that geographical isolation or host isolation or both may be sufficient to set in operation the processes of species formation, while the biotic environment plays an all important role in determining the rate and limits of this evolution. A disharmonic insular area with great gaps in its environment allows many non-lethal mutations to persist, whereas a fiercely competitive mainland environment rigidly rejects all but the best adapted, thus favoring adaptive evolution by natural selection.

The host-specificity displayed among some groups is astonishing. We find such great host-specificity among the plagithmysine longhorn beetles that if we find borings in a species of tree unrecorded as harboring a species of the group, we conclude that the borings are probably those of a new species. Thus, some new species of these beetles have been discovered, and others are known only from their borings and may be captured and described sooner or later. The same applies to certain genera of leaf-mining moths. Dr. Swezey has described a number of species which were worked out in the field on this basis. We can almost predict from a perusal of the literature where one might go and on what plant he might look to discover new species of some genera.

Perkins (1913:lxvii) says,

Very often, however, we find species, extremely closely allied, occurring habitually in the same locality and not geographically isolated. Thus, even within a few square yards, the three species of Longicorn beetles, *Plagithmysus darwinianus*, *P. lamarckianus* and *P. varians* occur. It is hardly conceivable that species can be more closely allied than these and remain distinct. Though so similar, the species keep quite apart. Each keeps to its own food-plant, and though occurring on adjoining trees the species do not mix nor interbreed. *P. darwinianus* has been found chiefly on *Sophora*, *lamarckianus* on *Pipturus*, *variens* on *Acacia*. We have observed great numbers of all these species in the field, but have never found even a stray specimen of one frequenting the tree affected by another or in company with it, even though these trees grew side by side. Thus these three species, though not geographically isolated, are isolated by their habits. I know no insects that could be more profitably experimented with by breeding in the field than these and other species of *Plagithmysus*.

The small leaf-mining *Philodoria* moths include at least six which are attached to the widespread endemic urticaceous tree *Pipturus albidus*. Most of these species are not known to overlap in distribution. Thus, one is known from Kauai; three from Oahu, two of which are restricted to small areas in different mountain ranges and one which is widespread; and two from Hawaii, but these occupy widely separated localities in different mountain ranges. Further collecting and study will probably reveal more species of this group localized in various places.

Giffard, in studying our leafhoppers, stated (1922:104) that

The distribution shows the value of segregation in species formation, which fact is also shown by the lists of food plants. Those species living on two or more plants show much greater variability than those confined to a single host. When we consider the topography of the islands, the isolated distribution of many plants and the fact that so many species are represented only by short-winged forms or only an occasional long-winged form, we can see how isolation can take place even on the same island.

I have been impressed by the adaptation of the color of insects to the color of the plants they frequent. The relationship is not confined to phytophagous species, but also occurs in predaceous species. In Hawaii even predaceous insects are frequently confined to particular hostplants. This color relationship does not appear to be correlated with protection, because for many of the groups in which it occurs we do not know of any particular predatory pressure great enough to have a selective influence. This is a problem about which we have little information. Perhaps predator pressures were greater than we realize in certain groups. However, we feel that some sections of the fauna were never brought under any great pressure by predators.

Near the summit of Haleakala on Maui, I found specimens of the pale, silvery-colored native *Geranium tridens* growing with their branches intermixed with those of the dark-leaved *Coprosma montana*. On the pale *Geranium* were colonies of a very pale *Nesosydne* leafhopper. On the dark foliage of the *Coprosma* was a black species of the same genus! Although the branches of the two shrubs intermixed, the two leafhoppers kept to their own hostplants.

The pale-leaved *Pipturus* has a long list of insects attached to it. Many of these are strikingly pale-colored. On the leaves of the same individual plant at the same time we may find pale delphacid leafhoppers, pale cicadellid leafhoppers, pale mirid bugs, pale psocids and a pale predaceous nabid bug. Near it, and perhaps with the branches intermingled, a dark-foliaged *Metrosideros* tree might be growing. On the dark foliage we may find dark-colored leafhoppers, psocids, mirids and nabids in the same genera. The palest of all Hawaiian nabid bugs is *Nabis kahavalu* (Kirkaldy), a pale-green species. It is found on the pale-green foliage of *Sophora*, and with it on Hawaii are usually found swarms of a mirid bug whose color matches the pale-green of the nabid perfectly. Although predaceous, the nabid is confined to *Sophora*.

Our *Proterhinus* beetles closely match the colors of their hosts. Reddish species are found boring in red fern-frond stalks; dark species are found on dark-barked plants, and pale species on pale bark. The nymphs of the foliage-frequenting *Paratrigonidium* crickets are generally green, but the terrestrial and bark-frequenting species are brownish. Perkins (1913:ccxvii) reported that one of these crickets is so highly host-specific that he found it on only one variety of the multiflorous tree, *Metrosideros polymorpha*.

Our widespread *Acacia koa* has a remarkable pair of delphacid leafhoppers attached to it. The so-called "leaves" of the *Acacia* are not true leaves but are modified stems, called phyllodes. True leaves are only produced early in the tree's life, or from more or less adventitious shoots. The finely divided true leaves are paler in color than the phyllodes. On the phyllodes we find *Nesosydne rubescens*. A closely allied offshoot species, *Nesosydne koae*, is found on the true leaves. Each of these species is restricted to its particular part of the same plant. Each differs in the color of its nymphs and adults to match more closely the differences in colors between the phyllodes and the true leaves. The adults of *N. rubescens* are a rather greenish-brown when living; those of *N. koae* are pale-green. *N. koae* lays its

eggs in young shoots; *N. rubescens*, whose ovipositor differs, inserts its eggs in the edges of the leaves and phyllodes. Here is an extreme case of isolation! These two species, although derived from the same stock, are structurally different; they live side-by-side on the same individual plant, separated only by the type of foliage they feed on; yet they maintain themselves as distinct entities.

A comparable case may be developed when the *Trioza* jumping plant lice (Psyllidae) are more carefully studied. As mentioned under *Trioza ohiacola* in my chapter including the psyllids, this species normally makes galls on the leaves of the hostplant. However, certain "abnormal" specimens have been collected from galls made on the stems. Perhaps the change of food indicates the beginning of a new form.

The long-legged dolichopodid flies are well developed in Hawaii, but they are comparatively poorly known. Dr. F. X. Williams has paid more attention to them than anyone, and the excellent information he has assembled indicates that a vast storehouse of ecological data remains to be uncovered concerning them. The species which hunt on the forest floor, those which are seen often on exposed patches of soil and those found on dull, shady tree trunks are dull-colored, usually brownish, species. The foliage-frequenting species often seen on large, green leaves in bright light tend to be greenish and bright-colored. The species which are found on dripping wet banks are likely to be bright metallic-colored to blend with their glistening surroundings. The species which frequent permanent streams are excellent and agile water skaters; those found on still ponds are fair to good skaters; but the species which hunt about areas where standing water exists only as temporary puddles, and the flies which frequent wet ground in the absence of standing water, are poor skaters.

Muir (1917:298) says:

I believe that one of the first steps in species formation among Hawaiian Delphacidae is a change of food-plant. In many cases this will lead to isolation and may eventually lead to differentiation of the germ-plasm. Mr. W. M. Giffard brought to my notice the fact that certain species feeding upon more than one food-plant have two or more forms. At Kilauea, Hawaii, *Nesosydne ipomoeicola* is very common on *Lythrum maritimum* H.B.K. and *Sadleria* sp.; specimens from the former plant are on the average much darker than specimens from the latter. In the same locality *N. blackburni* from *Clermontia parviflora* and *Stenogyne* has a distinct green tint when alive which is absent from specimens off of *Pipturus*.

It almost appears that these animals tend to assume a color which blends with the background color of the hostplants because of some inherent, unexplained factor acting within themselves. Some species appear to "feel uncomfortable" when they are on a background other than their chosen one. It is of particular interest that not only do different, but allied, species differ in color on their different hostplants, but that the same species have different-colored populations on different hostplants.

The endemic leafhopper genus *Dictyophorodelphax* is an unusual, aberrant offshoot of a normal type of delphacid leafhopper. The head is drawn out into a great prolongation almost unique among delphacid leafhoppers of the world. No

other Hawaiian group approaches them in this development. There are four known species, two on Oahu, one on Lanai and one on Maui. The entire group is restricted to plants of the genus *Euphorbia*. We expect that when other *Euphorbia* plants are examined carefully, especially on Molokai and Hawaii, additional new species will be discovered. Another noteworthy fact is that with one or two exceptions, none of the more than 130 known endemic delphacids is known to feed upon *Euphorbia*! A diverticulum of the gut is known to extend into the cephalic horn. Could this be associated with the type of food obtained from *Euphorbia*?

In the genus *Neseis* (a group of *Nysius* bugs), a compact group of forms has been segregated as the subgenus *Icteronysius*. All of these appear to be attached to the leguminous tree *Sophora*. These are the only bugs of 85 known members of the *Nysius* tribe in Hawaii which feed on a leguminous plant. The subgenus *Icteronysius* contains three subspecies, two found on Hawaii and one on Maui. It is of interest how the one on Maui was discovered. Usinger, in his monograph of the group (1942), stated that members of the subgenus would probably be found on *Sophora* elsewhere, and he left a request with Paul Baldwin, a National Park official, to search for *Nysius*-like bugs on *Sophora* on Haleakala, Maui. Baldwin complied with the request, and during an inspection trip found a new form, as Usinger had predicted. Other groups within the genus *Neseis* appear to have arisen through host isolation. There are four allied species including 12 subspecies all attached to *Pipturus*. A group of four species and six subspecific forms is attached to rubiaceous plants. Two allied species, one on Oahu and one on Molokai, have *Boehmeria* as their host.

Changes in habits may lead to entirely new evolutionary lines. Dr. Cooke tells me that in the highly developed Pacific land-snail family Tornatellinidae, a change from ground-dwelling habits to arboreal habits has almost always established new genera as a consequence. The drastic change from an aquatic to a terrestrial life has produced the most divergent of all the Hawaiian damselflies (see the discussion of *Megalagrion oahuense* on page 145). If this line could survive over a long period, a new order of terrestrial insect carnivores might be produced. The flightless hemerobiids (*Pseudopsectra*), discussed under flightlessness below, is a comparable case. If a population of any species can adapt itself to a new hostplant, it appears that a great advance toward a new form may have been made.

One of the principal facts which has occurred to me during my study of island life is that each problem must be considered as a unit in itself, for "laws" of wide scope do not always cover the multitudes of complex factors one meets. It is vastly different from the chemistry laboratory where we know that when we add "A" to "B" we will invariably get "C." The more years one spends on such study, the more involved the problems become and the more difficult it is to draw general conclusions.

In Hawaii we are dealing with relatively simple, disharmonic floras and faunas established in a favorable environment upon a rapidly changing substratum where environmental pressure (including predacity and parasitism) is reduced to a mini-

mum. Great impetus and momentum have been given to the processes of speciation by the peculiar set of circumstances here displayed. The end result has been great proliferation of species and generic complexes with much radiation and diversification. It is as if a great vacuum existed and species are rushing in to fill every available unoccupied niche. There is even the tendency for some species to enter into environmental categories foreign to their families or orders. New habits arise independently—the non-parasitic bees have developed parasitic species; the aquatic damselflies have produced arboreal species and an astonishing terrestrial species; delicately winged Neuroptera have given rise to flightless “monsters” encased in coriaceous, armor-like, non-functional fore wings, and which creep and leap about in search of prey; the drepaniid birds have rushed in to fill gaps and now are represented by slender-billed nectar suckers, grosbeak-like seed crackers, heavy-billed fruit eaters, sharp-billed insect catchers, those of almost woodpecker-like habits and others almost parrot-like in habit (fig. 46).

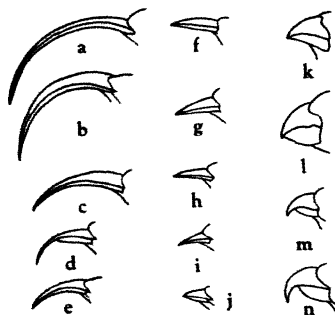


Figure 46.—Sketches of beaks of some drepaniid birds to show remarkable radiation within a single group of animals. *Loxops* (i) is considered nearest the ancestral type. a, *Hemignathus* (feeds on insects and nectar); b, c, *Drepanis* (nectar); d, *Heterorhynchus* (insects and spiders); e, *Vestiaria* (nectar); f, *Palmeria* (nectar); g, *Viridonia* (insects); h, *Himatione* (nectar); i, *Loxops* (mostly insects); j, *Ciridops* (palm fruits); k, l, *Loxioides* (mostly seeds); m, *Psittirostra* (fruits and seeds); n, *Pseudonestor* (wood-boring beetle larvae).

One of the most significant, if least heralded, of all discoveries relating to the Hawaiian biota is the finding of the terrestrial larva of the damselfly *Mcgalagrion oahuense* by my diligent, modest colleague, F. X. Williams. Who would have suspected that the nymph of this unique odonatan had, or could have, forsaken its ancestral aquatic habitat to take up a life completely foreign to its order and live on land? This species is the most divergent of its remarkable species complex. The nymphs, unlike those of any other known form, have adapted themselves to a life on land. They crawl about in search of their prey in the ground litter beneath dense clumps of fern (fig. 210 in vol. 2). The larvae are morphologically modified for such a life. The species has taken a great step from the typical aquatic habit of the Odonata. Is it not true that this peculiar species shows us how a new order of insects could arise? Here before us we have the essence of evolution. Given time, is it not possible that this unusual damselfly whose nymphs now crawl about on

damp ground could give rise to a new and distinct group of terrestrial carnivores? I believe so. To avoid repetition, the interested reader is referred to the section under *Megalagrion oahuense* and to the introductory statements under the generic heading *Megalagrion* in the chapter on the Odonata in volume 2 of this work.

I have studied an undescribed leafhopper from Oahu which carries a complete story in itself, I believe. Although obviously (that is, to anyone thoroughly familiar with the Hawaiian members of the family) it is merely a peculiar specific offshoot of a species of *Nesophryne* (Cicadellidae), this species has developed such peculiarities of its cephalic structure that it can hardly be placed in the same subfamily as the species from which it has been derived! In fact, it cannot be placed in its subfamily by the use of the well-known keys in current use. A new genus may have to be erected for this species, and some workers would probably have to remove it from subfamily association with its progenitors or specific associates, or they would have to modify the existing subfamily characterization. One could hardly blame the taxonomist for following such a course. The "blame" lies with the aberrancy of the species. My contention is that such a specific segregate may carry within itself the potentialities of an entire new group and that these potentialities may be exerted if proper isolation and time factors are brought into play. Within this single species lies a potential new genus, new tribe or an even higher category of an assemblage of diverse forms. Here again, then, is evolution in the act dramatically displayed.

When we study these large species complexes—*Nesophryne*, *Nysius*, land snails and others—we see that there is included a large amount of specific variability of the very characters which elsewhere are taken as generic. There are species which appear to be plastic and unstable. This great insular proliferation is conducive to segregation of atypical forms in what appears to be rapid progression. Most of these changes appear to be nonadaptive. The taxonomist has great difficulty in classifying the species and frequently does not quite know whether he is working with species within a genus or whether he should divide them into groups and call the groups genera. If he starts on the latter course, he may find, when a large amount of material is examined, that the way is blocked by intergrades. It is a puzzle.

A confusing problem confronts the taxonomist when he is faced with the necessity for determining the status of the forms of one species which have spread over several islands too rapidly to have outstanding characters develop on the various islands. For example, certain species of *Oliarus* leafhoppers appear to have occupied several islands in a geologically short period of time, and although the populations of each island are isolated and distinct, the differences between the various insular populations are slight in degree. Other series of forms which are apparently similar in basic make-up are more distinct and are presumed to be older. In the Hawaiian insects all extremes of this development can be revealed by study, for some forms are so distinct that they might be called genera by some workers, others belong to the rank of superspecies, others to species and subspecies, still others are difficult to classify and some may be called "varieties." Many of these

complexes defy explanation and definition, and we must ultimately accept the fact that each group, whatever it may be, must be studied and dealt with as a unit or set of units which has acted in its own way upon certain lines, and that general, over-all attempts at definition of evolutionary procedure, "laws" or "rules" are not feasible.

It is noteworthy that in some insect genera which are widespread in the Pacific, those species found in Australia with its continental environment and pressure are fewer in kinds and tend to be more stable and of more conservative nature. Out in Polynesia the multiplicity of species and their radical morphological diversity and aberrancy are astonishing. It appears that once unfettered in isolated insular environments the evolutionary potentials of some of these organisms are unleashed. This is particularly well displayed in the weevil genus *Microcryptorynchus*.

Displayed before us in the biota, there is every degree of differentiation from original ancestral stocks. Forms range from those, such as the strawberry, which have not been in Hawaii for a long enough time to become distinct from their immediate ancestors, to those which have hardly differentiated from their stem species and which may be exemplified by the short-eared owl, *Asio flammeus*, a Holarctic form, whose Hawaiian representative is called the subspecies *sandwichensis*. The Hawaiian hawk has diverged more from its parent stock, and it is considered a full species derived from *Butor swainsoni*. From these and similar examples in other groups, we might list a whole series of intergrades of increasing distinctiveness to end up with genera which are so unusually distinct that they cannot, with our present knowledge, be allied to any known group outside of Hawaii. The large genus of weevils, *Oodemas*, falls in this category, together with an extensive list of other genera which I shall not attempt to include here. The drepaniid birds, together with the amastrid and achatinellid land snails, were formerly classed as endemic families, but, with our expanding knowledge, we have learned that they belong to known families. However, they are apparently quite distinct enough to be called endemic subfamilies. Several groups are evidently distinct enough so that they may be assigned to endemic tribes.

With basic data from Mayr (1943), we may list some of the birds found in Hawaii in the order of their probable periods of invasion of Hawaii from the most recent to the earliest:

1. Black-crowned night heron, a non-endemic American form, but resident here.
2. Short-eared owl, an endemic subspecies.
3. Hawaiian hawk, an endemic species.
4. Hawaiian crow, an endemic species, but farther removed from its ancestral form than the hawk.
5. *Phacornis*, an endemic genus of thrushes.
6. *Moho* and *Chactoptila*, remarkable endemic genera of honey eaters derived from one immigrant.

7. Drepaniinae, a spectacular endemic array of highly evolved, widely radiated genera from a single immigrant.

Such facts as these show plainly that overseas immigration has been a continuous, long, slow process which has extended down to recent time.

Usinger in his study of Hawaiian *Nysius* bugs (1942:160) assembled his notes on this phase very nicely when he said,

All stages in the process of divergence may be seen at the present time. Thus the various species in the endemic genera fall into a series, ranging from (1) the widespread and variable *Oceanides nimbatus*, not yet broken up into distinguishable forms on the various islands, through (2) the scarcely differentiated *Nesais saundersianus*, to (3) the "polytypic species" (Huxley, 1938) or "Rassenkreis" (Rensch, 1929) *Nesais nitidus*, then to (4) the "supra-species" (Huxley, 1938) *Nesais hiloensis* (at least as regards the Molokai and Oahu forms), and finally to (5) that which Huxley (1938) has called a "geographical subgenus" and Rensch (1929) has called an "Artenkreis," namely the *Nesais mauiensis* and *fasciatus* group with allied species on the older islands.

INDEPENDENT ORIGINS AND DEVELOPMENT

From examples I have seen among oceanic organisms, there appear to be two major "types" of genera. One is a monophyletic line which springs from a single species and diverges from that base. The other is of polyphyletic origin, and the same "genus" may arise in two or more places at different times from different stem species. The monophyletic genus may be a very strong entity. The second type might be called a genus of the taxonomist who must have ways and means of grouping and classifying the myriads of population units confronting him. More often than not, he is unable to ascertain whether a group is monophyletic or polyphyletic. However, I do not feel that these sections are mere products of the taxonomist's imagination. Certainly, they are very real things, but genera vary in intensity as do species. Some genera are very "strong" segregates; others are weakly differentiated. It must be admitted that some are merely convenient, artificial or arbitrary assemblages created by taxonomists to enable them more easily to pigeonhole or separate ultimate units. Long periods of time and extinction of intermediate forms remove such categories as the last-mentioned one. A point I wish to make here is that in our island populations we have examples of both extremes as well as intermediates, that such developments are natural evolutionary products and that they do not exist in the minds of men alone.

As an example of a genus which has arisen from one species, we may cite our wonderfully developed *Megalagrion* damselflies. This local group is presumed to have developed from a single ancestral immigrant, and the descendants of that parent stock now form a local species complex.

The peculiar, flightless hemerobiid genus *Pseudopsectra* (figs. 47 to 51) is a good example of a genus whose members have not sprung from one stock but which have developed independently along similar lines to form a complex of flightless species with certain features in common. Some workers unfamiliar with the unusual local conditions and the history of this group might split several

of these flightless forms off as separate genera, but I doubt that such a procedure is necessary or desirable. The intermediate forms cause confusion. There are no intermediate forms between the volant ancestral stocks and the flightless derivatives, however. It is of interest that the name *Pseudopsectra* was chosen because there is a continental genus, called *Psectra*, in which the hind wings of the female have become abortive, indicating a similar trend but with less intensity than in our Hawaiian group.

The delphacid leafhopper genera *Nesorestias* and *Nothorestias* (see under Delphacidae), although making up compact genera, are each polyphyletic. *Nesorestias* contains 2 species, each of which has been derived from a different group of *Aloha* species. *Nothorestias* contains 3 species (one undescribed), and these all have been derived from different ancestral stocks.

H. B. Baker (1941:358) in discussing the development of the Polynesian microcystine land snails said:

While, in general, their distribution and relationships conform with the theory of evolutionary divergence, certain remarkable convergences almost look as if some branches of their subfamily tree had inoculated and produced stocks of double origin. For example, some species of both *Philonesia* and *Hiona* develop a left shell lobe in the Hawaiian islands, although this structure is not produced in any of the other Microcystinae except *Kusaiea frivola* [from the Caroline Islands] and *Lamprocystis moalana* [from Fiji]. Again, the epiphallus in the species of *Hiona* (subgenus *Insularis*) from the Society Islands considerably resembles that in the species of *Lamprocystis* (subgenus *Aturua*) from the Society and Cook Islands and that in the genus *Microcystis* from the Cook and Austral Islands. While the production of a new line by hybridization of such divergent animal stems seems to have happened rarely, if ever, in nature, it might be most apt to occur if members of related island groups were accidentally brought together. Because the forms of each island are geographically segregated, divergence may result from lack of interbreeding but does not require functional inability to produce such crosses.

Usinger (1942:119) notes that in the *Nysius* bugs of Hawaii a "wider range of characters is exhibited... than in the combined *Nysius* fauna of the rest of the world. Such characters as form of bucculae, length of rostrum, and shape of costal margins, which are fairly reliable guides to genera elsewhere, break down completely in the various extreme species of Hawaiian *Nysius*." Similar statements can be made for many of the better-developed groups of Hawaiian insects.

A number of species from several geographical regions, and which have not had a common ancestry, have been assigned to the psyllid genus *Kuwayama*. This genus is obviously polyphyletic, and the species assigned to it appear to have developed their combination of characters independently from the widespread genus *Trioza* or one of its derivatives. Some of the Hawaiian species show a tendency to revert toward the ancestral *Trioza* type.

Parallel development appears to have occurred among the prosopid bees, because it is improbable that the European and Asiatic species which can be assigned to *Nesoprosopis* have the same ancestry as the Hawaiian assemblage.

Among the tornatellinid land snails, *Lamellidea tantalus* from Hawaii has been almost duplicated by a species in Rapa, about 3,000 miles away at the opposite end of the distribution of the family in eastern Polynesia. Although these two

species have assumed shell characters which would appear to place them in the same genus, their internal anatomy indicates that they belong not only to distinct genera but to different subfamilies! Both species live under lichens on the bark of trees.

The ground beetle genus *Colpodcs* (widespread in the Pacific) has given rise in Hawaii to some species which Dr. Sharp (1903) referred to the non-Pacific genus *Platynus* because they so closely resembled certain American *Platynus*. The superficial resemblance is due entirely to a parallel development, and the two groups have no close affinities.

The only endemic bees found in Hawaii belong to the hylaeid genus *Nesoprosoapis*. We believe that the present complex of 55 forms has arisen from a single immigrant Asiatic stock. This local complex has developed species and groups of species which have radiated from the stem form to such a degree that they might have been called different genera had Perkins not assembled such careful data on their interrelationships. However, the most remarkable group is one which has independently developed commensal or semi-parasitic habits. Five allied species which have sprung from a single stem species constitute the semi-parasitic group. The normal-type bees store honey and pollen on which their young feed, but the commensals have lost their industrious habits and lay their eggs in the fully provisioned nests of certain industrious species. The females of the industrious species have well-developed structural modifications which aid them in gathering pollen, but in the commensals these structures are degenerate. Two principal nesting sites are chosen by the industrious species. Some species make their nests in burrows in the ground, others make theirs in hollow stems or in wood and some utilize both situations. Peculiarly, the semi-parasitic forms attack only the nests made in the ground. Although they are not host-specific and may lay their eggs in the nests of more than one host species, they are not known to attack nests other than those made in the ground.

There is a greater development of *Odynerus* wasps in Hawaii than in any one area inhabited by this nearly cosmopolitan genus. Most of our species utilize existing holes, such as old beetle borings and crevices in rocks, for nesting sites or they bore into wood or burrow in the soil. However, *Odynerus oahuensis* Dalla Torre is unique, because it has become an insect potter and has developed the habit of building complete, free, mud cells. "It is distinguished for its architectural ability, standing alone in this respect among the Hawaiian Odyneri whose nesting habits are known. Nor does this habit appear common among *Odynerus* in other parts of the world." (F. X. Williams, 1927:453.) A similar, free, mud cell was found on banana at Kipahulu, Maui, by Dr. Swezey, but its maker remains unknown.

Many insects the world over have developed flattened bodies better to fit themselves to their environment. Fleas are laterally compressed to enable them to slip between the hairs of their hosts. Many kinds of insects are dorso-ventrally depressed to enable them to forage beneath close-fitting dead bark of trees. Among

our endemic delphacid leafhoppers, there is one species, *Nesodryas freycinetiae* Kirkaldy, whose nymphs have become independently modified to enable them better to live between the closely fitting leaf blades of the climbing *Freycinetia* vine. Of all of the 139 native delphacid leafhoppers, this is the only one I know which has developed a flattened nymph.

In the crane fly family (Tipulidae), one Hawaiian species has developed a habit which, insofar as is now known, is unique for the entire group. The larvae of our *Limonia foliocuniculator* (Swezey) (Swezey, 1915:87) mine the living leaves of *Cyrtandra* (Gesneriaceae). Tipulid larvae mostly dwell in the soil or in decaying vegetation, and some are aquatic. The leaf-mining habit is a remarkable new development.

A similar abnormal development has taken place in the large weevil genus *Proterhinus*. The normal larval habit of these species is to bore in dead wood or dead bark. However, at least three species have developed leaf-mining habits on Oahu. One of these mines the leaves of *Astelia* (Liliaceae); the other two attack *Broussaisia* (Saxifragaceae). Another species bores in the living stems of *Broussaisia*.

The true bugs of the genus *Saldula* (shore bugs) are mostly riparian in habit. One unusual species is reported to inhabit dry heaths in Europe. In Hawaii, however, species have developed arboreal habits. It is quite a surprise to one who has collected these bugs along stream and lake banks of a continent to come to Hawaii and beat them out of shrubs and trees!

The endemic leafhopper genus *Dictyophorodelphax* is unique in that it has developed a great prolongation of the head (see the figures under this heading in volume 4 of this work). This gives the species the appearance of such fulgorids as *Scolops*, and although the genus is closely allied to other Hawaiian genera, it has quite a different appearance.

The spectacular radiation and development of new types among the drepaniid birds has already been referred to (fig. 46).

It is noteworthy that many of the derived forms of the Hawaiian fauna are much more restricted in range and habit and are much more sensitive to change than are those which most closely resemble or represent the original stock. As an example, the native land birds most successful in meeting changing modern conditions are the *Chasiempis* flycatchers, geologically the most recent of the perching-bird invaders of Hawaii. The old, specialized drepaniids have been vanishing with startling rapidity since white man colonized the islands.

FLIGHTLESSNESS AMONG HAWAIIAN INSECTS

Endemic development of flightless species has occurred in the Orthoptera, Thysanoptera, Heteroptera, Homoptera, Neuroptera, Lepidoptera (?), Coleoptera, Hymenoptera and Diptera. Some remarkable examples of independent loss of the powers of flight exist here. Perkins (1913:xlvi) has given an excellent review of the subject, and I shall refer only to some of the problems and a few of the examples.

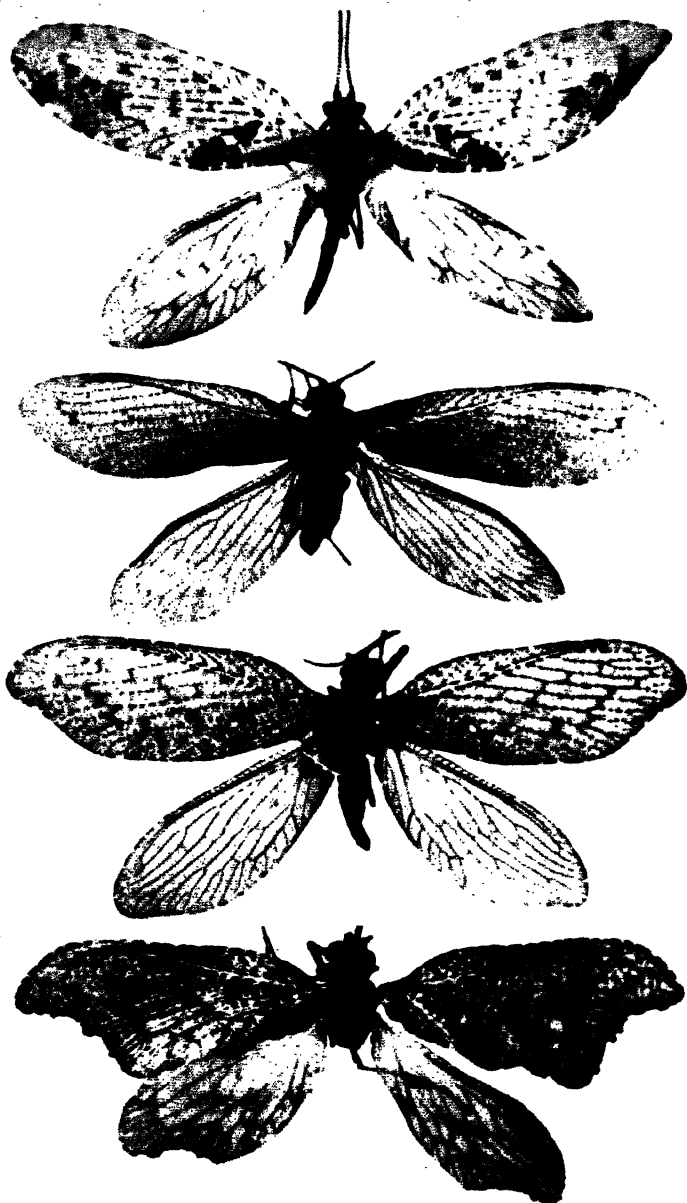


Figure 47.—Four species of *Nesomicromus* to show the transition between the rounded wing tip (top) and the angular type (bottom), for comparison with the accompanying illustrations of the flightless derived hemerobiids. According to the opinion now held, several of the flightless species appear to have evolved independently from such varied types of ancestors as the types figured above. From top to bottom the species are: *Nesomicromus bellulus* Perkins (the right fore wing is slightly turned under at the apex), *N. rubrinervis* Perkins, *N. vagus* Perkins, *N. species near drepanoides* Perkins.

I cannot believe that selection has caused the loss of wings because winged individuals are likely to be blown off the islands. These islands are not mere rocks. I concur completely with Perkins' statement (1913:1):

Nearly all the flightless endemic insects are inhabitants of the forest, or if they frequent exposed situations like some of the Carabidae, they are closely related to species that frequent thick forest and are equally flightless. There is no ground for supposing that in these islands, as has been suggested for flightless insects inhabiting other Oceanic islands, the wings have been lost or degenerated through the agency of natural selection, as being a source of danger, if used on small land areas, where flying insects are supposed to be liable to destruction from being blown out to sea.

The development of our flightless species appears to have come about through the survival of individuals with hereditary abnormalities. They have not been selected because they are better fitted—they have been fortunate in being developed within a friendly environment with quantities of food so easily attainable that the loss of the powers of flight has not been a form of "lethal mutation," and they have had no enemies which might overwhelm them. Certain mutant forms with aborted wings can often survive simply because they do not need wings to get about and to get their food. They need not travel far to obtain what they need and to procreate. It is the ability of certain flightless forms to survive, rather than selection acting against flight. It is probable that had these mutant forms occurred in the rigorous environment of a continental area, they would not have survived. Our present human society harbors, feeds and protects the feeble of mind, the maimed, the chronically ill and the blind. These individuals would have had little or no chance of surviving in environments in which human society existed not so very long ago. The flightless insects of Hawaii are the descendants of cripples which survived only because in these insular environments biotic and environmental pressures are reduced to a minimum, and conditions have been favorable for their survival. They are "hopeful monsters" arisen under circumstances in which there is hope.

Some of these flightless species which were successful under primitive Hawaiian conditions have recently succumbed to new biotic pressure brought about by the introduction of predators which are foreign to the Hawaiian biotal balance. Some of us have searched intensively under the very trees where Dr. Perkins procured a series of the flightless fly *Emperoptera mirabilis* Grimshaw but have never been able to find a single example of the species. It appears that this remarkable fly is now extinct—at least in the type locality—because it was unable to withstand the new pressure created by the invasion of its environment by immigrant predaceous ants.

Flightlessness is not something which has occurred rarely and which developed single lines of flightless forms, but flightless species have arisen within the same group of Hawaiian insects at different times and at different places. Also, flightless species have arisen locally from flightless species whose ancestors in turn were fully winged. The flightless *Emperoptera* fly described from Perkins' Oahu collecting arose independently and from quite a different stock from the one I de-

scribed from the deep highland rain forest of Maui (Zimmerman, 1938:145). Lamb (1909) described another in the same family from the subantarctic islands of New Zealand. The remarkable flightless *Nabis* bugs appear to have arisen from several local stocks (see the text under *Nabis* and the illustrations in volume 3 of this work). I have chosen the flightless lacewings (Neuroptera: Hemerobiidae) to illustrate this section.

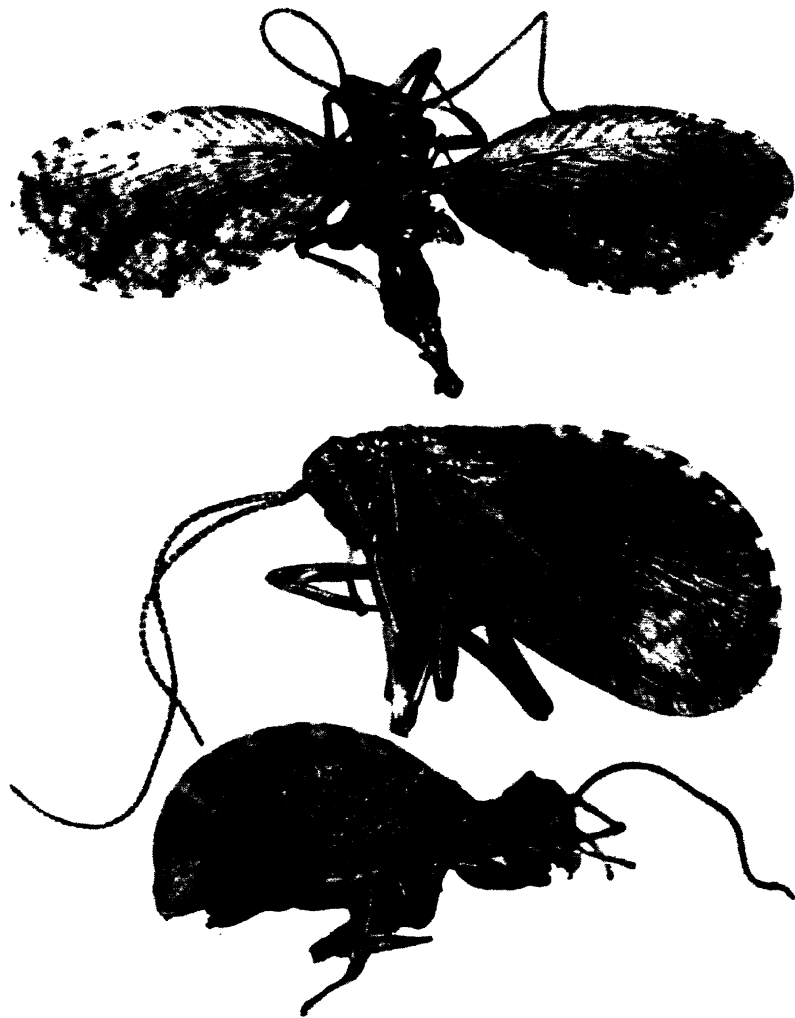


Figure 48.—Flightless endemic Hemerobiidae: *Pseudopsectra lobipennis* Perkins, top and middle; *Nesothauma haleakalae* Perkins, cotype, bottom.

There have been six species of flightless hemerobiids discovered in Hawaii. One of these is from Kauai, one from Oahu (undescribed because the material was lost in the field and it has not been re-collected), three from Maui and one from Hawaii. These species are very distinct, one from the other, and each appears to have developed from a different ancestral *Nesomicromus* (a large endemic genus) at a different time and at a different place. The species of *Nesomicromus* fall into two main groups on the basis of the shape of the fore wings. One group has the



Figure 49.—*Pseudopsectra cookcorum* Zimmerman, a flightless hemerobiid with unusually well-developed, specialized setae.

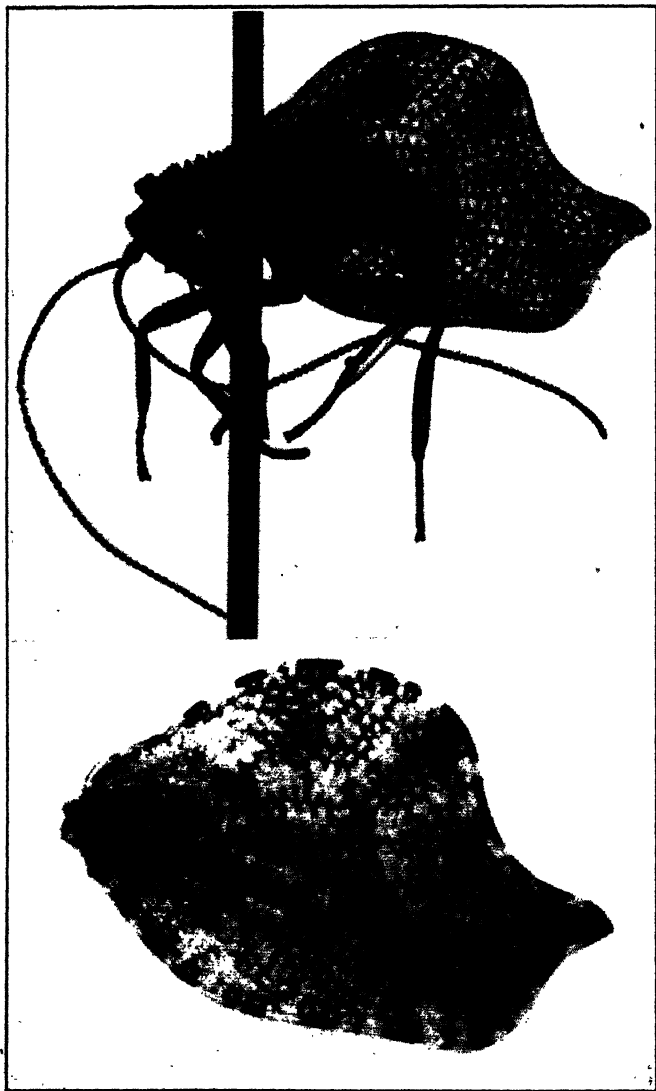


Figure 50.—*Pseudopsectra swaseyi* Zimmerman, a flightless hemerobiid with peculiar angulate wings which are unusually coarsely net-veined.

apices of the fore wings rounded; in the other group the margins are concave, at least at the apex, and some of those with the concave apices also have the posterior margins sinuous. The former group is the more abundant. The illustrations (fig. 47) represent these groups clearly. The remarkable *Pseudopsectra swezeyi* Zimmerman has arisen from an angulate winged ancestor, but all of the other species have arisen from the section with rounded wings. On the five described species of *Pseudopsectra*, the hind wings are reduced to minute fleshy flaps. On the single *Nesothauma*, no hind wings can be found. The length of the hairs of the body and wings varies among the various species of *Nesomicromus*. On some the hairs are conspicuous, but on others they are minute and are hardly discernible. The same applies to the flightless derivatives, but a further advance is made. On *Pseudopsectra cookorum* Zimmerman the fine hairs have developed into very large, rather grotesque, bipartite spines (see fig. 49).

The volant *Nesomicromus* fly from plant to plant in search of prey. The flightless species crawl about on mossy logs and limbs and frequent low foliage in their food hunting.

The wings of the volant species are delicate and lace-like, but the flightless species, in addition to having their hind wings abortive, have the fore wings



Figure 51.—*Pseudopsectra usingeri* Zimmerman, a flightless native hemerobiid with rounded wing apices.

reduced and greatly thickened. The venation is confused with the veins thickened and with multitudinous cross-veins. The wings tend to be heavy, coriaceous shields for the body and are not a far cry from the elytra of beetles. It is of interest that a rather similar tendency to coriaceous wing development is displayed by our flightless endemic *Nothorestias* delphacid leafhoppers—a group in an entirely different order.

Given time and opportunity, one or more of these grotesque “hopeful monsters” might well give rise to a successful new descendent line which might evolve further into a distinctive new group. One can visualize what might happen if a single gravid example of one of these extreme species were to be carried to and left undisturbed through a long period of time on a new archipelago of high islands which had an array of unfilled ecological niches and was uninhabited by competing groups or overwhelming enemies. Here, again, is displayed before us dynamic evolution carrying the same potentialities which have given rise to the world's floras and faunas, present and past. Here is the way a new order of organisms might arise.

PREDACITY AND PARASITISM IN THE ABORIGINAL FAUNA

As we should expect, the predator and parasite pressure in an insular area such as Hawaii is comparatively low. It is low because of the great difficulties involved in overseas dispersal and colonization. It has been only of very rare occurrence that phytophagous organisms have managed to cross the sea and become established here, and rarer still have been the successful invasions by predators and parasites. The arrival of predators and parasites without the previous establishment of suitable hosts obviously would lead to the early death of any successful immigrants. One would not expect that insect predators and parasites could accompany the original colonizations of their insect hosts for obvious reasons—the most important of these is the small number of hosts arriving at any one colonization period. A single bird immigrant might bring with it lice, mites and worms which could be passed on to its young because of the parental care necessary to rear them, but this would not be true of insects.

There is a sequence of events which much be followed in the population of any new island. Very soon after emergence from the sea, certain of the cryptogamous plants are able to establish themselves. Then, as the rock disintegrates under rain, wind and plant action, higher plants slowly become established as conditions become suitable for their survival. Ecological niches for a large number of kinds of plants do not become available until a long period of time has passed. Conditions change rapidly in the nature and complexity of the new forest as new kinds of plants become established and begin to spread. Only after suitable hosts have occupied the area can animals become established. One would expect that land snails would be among the first land animals which could find food and shelter on a new island. Certain insects, such as some of the small lichen-feeding moths, would be the first to be able to thrive. The speed of development of the biota would increase geometrically with time. Carnivores and parasites could not become established until

suitable hosts were fairly well developed in numbers and in area, but it usually does not require much time for a newly immigrant species to increase to large numbers if there is an adequate food supply.

The predaceous groups of insects in the endemic fauna are as follows:—

Odonata: The dragonflies *Anax* (1 species), *Nesogonia* (1) and *Megalagrion* (27) feed mostly on aquatic insects and on insects which accidentally fall into the water. It is improbable that the pressure they brought on the endemic insect fauna influenced speciation.

Heteroptera: *Oechalia* (15 species) (Pentatomidae) prey upon various caterpillars, and some also attack certain leafhoppers. They are a rather restricted group. Only a few (2?) reduviid species are native. The Nabidae, however, contain a large complex of *Nabis* species (25 described) which are the most important of the predaceous Hemiptera. Only a few Anthocoridae are endemic (*Lasiochilus* 5, *Lilia* 1), and these probably prey upon such insects as psocids and thrips. The Saldidae (6 species of *Saldula*) are rather local insects.

Neuroptera: The 26 *Anomalochrysa* chrysopids and the several genera of Hemerobiidae (27 species) feed upon psocids and Hemiptera. It is doubtful that the predator pressure of this group was ever very great.

Coleoptera: The Carabidae (about 215 species), Staphylinidae (90) and Histeridae (35) are the only well-developed predaceous groups in this order, and only a few predators in other families of beetles are native (Dytiscidae, 2 species; Hydrophilidae, 2; and Cucujidae, probably less than 15). The predator pressure brought by the Carabidae and Staphylinidae was a dominant one.

Hymenoptera: The fly-catching Mimesidae and Crabronidae number only about 32 species. The mimesids prey principally upon leafhoppers, whereas the crabronids appear to have fed largely on the calliphorids, the larger *Drosophila*, Dolichopodidae and Anthomyiidae. The eumenid *Odynerus* are numerous both in species and in numbers; their prey consists of certain kinds of caterpillars, and they may have exerted a fairly high pressure on certain moths. It is of interest that these wasps prey almost exclusively on the Pyralidae and certain of the Microlepidoptera; rarely do they attack the Geometridae, which are so abundant in our forests.

Diptera: The only predaceous flies of account are the Dolichopodidae and the *Lispocephala* anthomyiids. There is an extensive series of genera and species of dolichopodids in the native fauna, and they prey principally on larvae of other flies, small caterpillars and perhaps on other organisms. We have little knowledge of their prey. The large genus *Lispocephala* feed as larvae upon the larvae of other flies such as the tipulids, and the adults feed on various insects, even members of their own genus.

Other predators of insects include:—

In addition to the insects, a rather large series of native spiders constituted a general group of predators.

Some of the native birds also fed on various insects. Among the more important insectivorous birds are the five thrushes, which at times feed upon spiders and caterpillars, especially the Geometridae. One of the Kauai forms, though largely frugivorous, hunted *Rhyncogonus* weevils and is the only known bird that fed on these insects.

The three *Chasiempis* flycatchers feed upon a large variety of insects and other organisms including flies, beetles, beetle larvae, moths, caterpillars and even myriapods. They not only catch insects on the wing, but search for them on foliage and on limbs and dead wood. These birds are, relatively, newcomers to the islands.

The drepaniids generally take insects such as caterpillars and moths and some spiders on occasion, and all of them feed their young on insects and spiders. *Loxops*, *Oreomyza* and *Heterorhynchus* are largely insect-eaters, but some of them also take nectar. *Loxops* and *Oreomyza* feed largely upon caterpillars and spiders and at least an Oahu *Oreomyza* is known to have searched especially for certain carabid beetles. *Heterorhynchus* fed upon spiders and caterpillars and was especially fond of *Oodemus* weevils. *Pseudonestor* fed particularly on the immature stages of plagithmysine beetles on Haleakala, and was specialized for tearing open branches and twigs in search of its prey. *Viridonia* preyed extensively on the cricket, *Paratrigonidium freycinetiae*, on Hawaii.

The Kauai "Oo" (*Meliphagidae*) fed on caterpillars and the native prognathogryllid and *Paratrigonidium* crickets, and the other species of the genus took insects on occasion.

The single Hawaiian bat is an uncommon species, and almost nothing is known about its food habits.

The only insectivorous plant we have is *Drosera*, which is confined to a few high mountain bog areas. No survey of the insects it captures has ever been made. It is known to trap large numbers of flies.

The parasitic insects in the native fauna are as follows:—

Hymenoptera: In the Ichneumonidae, *Agrypon* (11 species), *Echthromorpha* (1) and *Enicospilus* and its allies (31) are all parasites of moth caterpillars.

The braconids have only a single species of *Ecphylopsis* which parasitizes long-horn beetle larvae, and its endemicity may be questioned.

In the Encyrtidae we have a series of *Anagyrus* species (7 described) which are parasites of mealybugs; *Coelopencyrtus* has 4 species which parasitize *Odynerus* wasp larvae; *Hypergonatopus* (7) are hyperparasites of the two native dryinid wasps; *Xanthoencyrtus* (6) are mealybug parasites.

The eupelmids (*Eupelmus*, 54 species, and *Lepideupelmus*, 3) have developed one of our two largest endemic parasite complexes, and they have radiated out to parasitize such varied hosts as Hymenoptera, Diptera, Orthoptera, Neuroptera, Lepidoptera and Coleoptera; some are egg parasites, others are parasites of larvae.

The Miscogasteridae contain about a dozen species about which little is known. One has been recorded as a parasite of a *Dryophthorus* weevil.

The Mymaridae are represented by 16 species of *Polynema* which are, or are presumed to be, parasitic on the eggs of delphacid and cicadellid leafhopper eggs. A species now considered an immigrant attacks the eggs of an immigrant *Nabis*.

The Diapriidae contain 9 species centering around *Phaenopria*, and those which are known are parasites of *Drosophila* larvae.

The Scelionidae include six species of *Prosanteris* and five of *Microphanurus* (endemism uncertain); at least one of these species has been reared from *Nysius* bug eggs.

Our Cynipidae, *Eucoila* (9 species) and *Colthonaspis* (18 species), are parasites of *Drosophila* larvae.

In the Bethyliidae we have 16 species of *Sclerodermus* which are parasites of wood-feeding caterpillars and a few are parasites of certain wood-boring cerambycid and, possibly, other beetle larvae. *Sierola* constitutes the largest complex of native parasites, for it contains 181 known species. These are parasites of moth caterpillars.

The Dryinidae have only two (1?) native species of *Pseudogonatopus*. These are parasites of delphacid leafhoppers. They in turn are parasitized by *Hypergonatopus*.

In addition to these, there are a few species of Spalangidae, Aphelinidae and Eulophidae which possibly might be native; these are known only from seven species placed in six different genera in the three families.

Diptera: The only parasitic Diptera in the native fauna are the pipunculid flies, 12 of which are known, and these are all parasites of delphacid leafhoppers.

Although much work remains to be done on the relationships of the endemic predators and parasites, particularly by breeding to associate properly the known species with their hosts, some generalizations can be drawn from the data at hand. Some large sections such as the Carabidae, Staphylinidae, Histeridae, Nitidulidae, Elateridae and possibly other groups—over 500 species of beetles alone—are not known to have any insect parasites. Also, these and other families have no known predators in the adult stages, excepting some negligible feeding on occasional species by a few birds and, possibly, damselflies. The large *Odynerus* wasp complex of more than 100 species has some of its species attacked by a few species of *Eupelmus* and *Coclopecyrtus* wasps, and these are the only certainly native parasites known to attack them. Members of the largest complex of Hawaiian Diptera—the Dolichopodidae—have no known parasites, and, at most, only a few predators ever attack the adults (certain crabronid wasps catch some species and others are probably occasionally taken by *Lispocephala* flies and Odonata). I have not found a record of any native parasites of the species of our well-developed *Nabis* bug complex, although Perkins (1913) suspected that one or more egg parasites possibly occurred. If the group has any insect predators, attack must be only occasional. One would expect to find parasites of the exposed eggs of our endemic pentatomid bugs, but none has been found. Only a single parasite species (*Microphanurus*) has been reared from one species out of our nearly 100 endemic lygaeid bugs. Many eggs of various species have been reared with-

out a parasite having been found. The groups which are known to be most subject to the attack of endemic parasites and/or predators are the delphacid and cicadellid leafhoppers, Pseudococcidae, Lepidoptera generally, the wood-boring beetles such as the Anobiidae, Ciidae, Cerambycidae, Aglycyderidae and Curculionidae, the nematocercous Diptera and *Drosophila*.

In the light of present knowledge, it appears reasonable to conclude that parasite and predator pressures have not played a major role in species formation in Hawaii.

CENTERS OF DEVELOPMENT WITHIN THE ISLANDS

One of the most fundamental facts in distribution within the islands is that the various islands have a differential development of species in many genera. Some genera are extensively developed on one island only, some on two or more adjacent islands, or they may be highly developed on one island and become progressively fewer in numbers from one island to the next adjacent and the next. Each of the larger islands has its various developments of different groups of insects which indicate that each island was colonized individually and that different groups arrived at different times on different islands. This is one of the soundest principles which argues against these islands ever having been connected in one mass. I interpret such distributions to mean that the areas of greatest development indicate the place of origin within the Hawaiian Islands of the species complexes in question. For example, genus "A" first became established on Maui where it spread and developed a complex of species. Because of the ocean barriers, few individuals ever became established on the neighboring islands of Hawaii and Molokai. However, through the ages, some forms did become established on these islands, and today we have a large complex on Maui, a smaller one on Molokai, and a yet smaller one on Hawaii. The island of Molokai is closer to Maui than is Hawaii, and hence it was colonized more frequently than Hawaii and now has a greater number of species than Hawaii.

TABLE SHOWING EXAMPLES OF DISTRIBUTION PATTERNS

GROUP	NUMBERS OF SPECIES				
	Kauai	Oahu	Molokai	Maui	Hawaii
<i>Mecyclothorax</i> (beetles)	0	6	20	40	17
<i>Bembidiini</i> (beetles)	14	5	4	5	1
<i>Metromenus</i> (beetles)	3	17	5	1	1
<i>Cossoninae</i> (beetles)	29	22	3	15	6
<i>Achatinella</i> (molluscs)	0	125±	0	0	0
<i>Partulina</i> (molluscs)	0	2	23	44	6
<i>Newcombia</i> (molluscs)	0	0	9	1	0
<i>Carelia</i> (molluscs)	28	0	0	0	0
<i>Rollandia</i> (plants)	1	18	0	0	0
<i>Stenogyne</i> (plants)	4	2	3	14	28
<i>Phyllostegia</i> (plants)	6	12	6	15	9
<i>Psychotria</i> (plants)	3	1	0	0	0

The distribution patterns are not at all similar. In some groups, Maui has the greatest development, in others Oahu is the center, while other complexes are best developed on Kauai, Molokai or Hawaii. Thus, it is apparent that each of these islands has shared individually original colonizations or developments and each has acted independently in this regard. These developments are quite independent of ecological conditions, because for the most outstanding examples of these developments equivalent conditions exist on all the major islands.

The accompanying table was prepared to illustrate some examples of this phenomenon. The islands are listed in order from west to east.

DISTRIBUTION OF SPECIES WITHIN THE ISLANDS

Endemic organisms in Hawaii range in distribution from restricted micro-niches to widespread. Some species occur only in certain valleys or in confined parts of valleys. Some species occur throughout the range of their hosts. The distribution of some species appears quite independent of ecological conditions; other species are distributed in accordance with strict ecological requirements. Questions to make one ponder are such as why the strong-flying Hawaiian crow is absolutely confined to a certain restricted range on part of one island, yet some wingless insects are found widespread on all of the main islands. Why has the Hawaiian hawk restricted itself to the island of Hawaii, and although it occasionally straggles to the adjacent great island of Maui, why has it never colonized that island? (This hawk has wandered all the way to California.)

An interesting fact is that most of our native insects, both winged and apterous, are confined to single islands and most often to restricted ranges on those islands. Some of the newly introduced species, however, whether they be beetles, flies, wasps or bugs, have spread rapidly, not only over entire islands, but have crossed the open-sea channels between the islands and, in many cases, have established themselves on all of our main islands within a few months or a few years. Man has had much to do with this inter-island dispersal.

The remarkable, restricted ranges of most of the native species of Polynesia are in rather marked contrast to the distributions of certain insects which I have studied from the Malay Archipelago. In those continental fragments, I have noted that the insular endemism is much lower than it is in Polynesia and that many species are widespread throughout many islands.

For an example of the distribution of a genus on one island, we may choose the genus *Rhyncogonus*, which is composed of the largest of all Hawaiian weevils. Indeed, they are among the largest, most conspicuous and most sought of all, the Hawaiian beetles. They are such prizes that collectors never pass them by; even snail collectors and botanists bring them in for the entomologists. There are few Hawaiian genera which have received such careful attention as has *Rhyncogonus*. Only one new Hawaiian species has been collected in the past 20 years. Dr. Swezey has given the genus special study, and has plotted the distribution of the 13 species found on Oahu. His map is reproduced here as figure 52.

Most of the species have been taken at altitudes between 1,000 and 2,000 feet. Each species occupies a discrete locality, and no two species are known to overlap in distribution. The adults are wingless, and they feed upon leaves of various plants. The eggs are deposited on leaves, and upon hatching, the young larvae drop to the ground into which they burrow (to feed upon roots?).

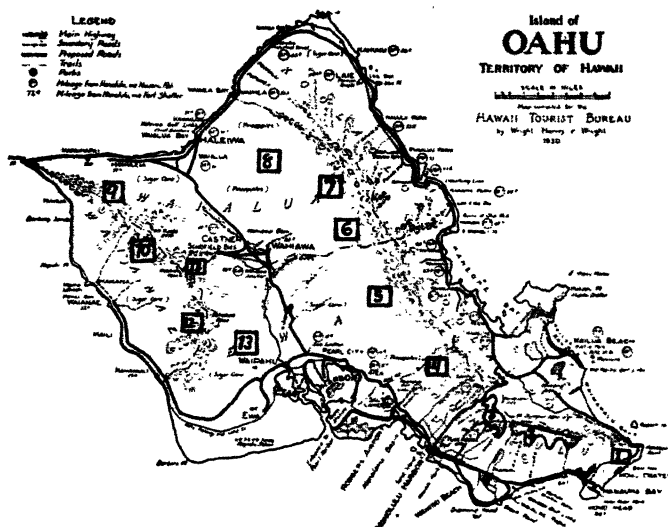


Figure 52.—Map showing the distribution of the known species of the weevil genus *Rhyncogonus* on Oahu. No two species are known to overlap in range. Most of the colonies have been found at altitudes between 1,000 and 2,000 feet. 1, *Rhyncogonus simplex* Perkins; 2, *R. koebelei* Perkins; 3, *R. blackburni* Sharp; 4, *R. mutatus* Perkins; 5, *R. obsoletus* Perkins; 6, *R. segnis* Perkins; 7, *R. freycinetiae* Perkins; 8, *R. oleae* Perkins; 9, *R. fuscus* Perkins; 10, *R. funereus* Perkins; 11, *R. saltus* Perkins; 12, *R. welchii* Perkins; 13, *R. extraneus* Perkins. (After Swezey, 1934.)

ARE THESE INSULAR SPECIES WE ARE STUDYING "GOOD SPECIES"?

Some workers (not systematists) have questioned the "degree" of our species, and they wonder if we are really dealing with "full species" or "good species." It should not take long for anyone who really investigates our species to ascertain that we are dealing with full species and good ones. Many of our groups of species contain such distinct forms that some of them would not be placed in the same genera by workers unfamiliar with the intermediate or connecting species or who might be working with small collections. During the course of this work, an authority examining two allied species of a genus for me stated, after superficial examination, that they belonged to two distinct families. After being informed that our local data indicated that they were allied species, he checked more fundamental characters and agreed with me. One can easily be led astray by these

insular products. I have little doubt that if the Hawaiian *Drosophila*, for example, were large animals like birds or rodents, they would be segregated into a large number of genera and even higher categories on the basis of their conspicuous morphological differences. The same applies to most of our species complexes. Our heavy-billed drepaniid birds were once described as finches because of the confusing morphological similarities in form of beak. Although they are not finches, they have taken over the form and habits of finches and have filled an empty niche in Hawaii.

To take only favourite classificatory characters of Passerine birds, form of the bill and structure of the tongue, we have here forms with long curved bills, forms possessing bills of an average insectivorous shape, thin finch-like bills, bills recalling that of the pine-grosbeak, and heavy haw-finch-like bills. Not less diversified are tongues, from fleshy tongue recalling that of a bullfinch and every kind of gradation towards bifid and fringed tongues. Quite as much diversified is the structure of the nostrils. In all, the diversity is so great that it may seem advisable to separate the long billed genera and to include the others perhaps with the *Fringillidae*. But Prof. Gadow has demonstrated that all these birds form but one family. I came to the same conclusion after my studies. And I consider that all these distinctive characters are adaptive, presenting several widely diverging lines of adaptive radiation, corresponding to great variety of biology and diet of *Drepanidae*.

On the Galapagos we find another peculiar group first discovered by Darwin and described by Gould. At present they are considered as forming one genus, *Geospiza*, with about 25 species. By their rather heavy, short-tailed build, by their colour and patterns, and by colour variations depending on age, they are extremely uniform. But the variety of bills is astonishing and also different is said to be their biology. And at the same time, the gradations of the shape of the bills are such as to make an establishing of divisions quite senseless. (Sushkin, 1929:375-376.)

Many species have outstanding differential characters, but with the multitudes of species, connecting intermediates may, in many instances, be found. Extinction within the ranks would result in large numbers of species groups or genera. It must not be overlooked, however, that various species are known to have large numbers of subspecific forms. Some of these now recognized in lesser categories were earlier classed as species. But we can recognize those groups, and when we now speak of species, I believe that in most cases we know fairly well what we are dealing with. Some groups of allied forms, however, are difficult to understand, and only critical study and experimentation will reveal the true nature of such forms—if they can be understood by us highly evolved human beings so far removed from the creatures we are studying. Since this was written the following material from the pen of Dobzhansky (1944:251) has come to hand and is worthy of being quoted:

The opinion is often expressed that species and races are arbitrary categories. This opinion is false. If given the opportunity to secure the necessary data, a biologist is able in a majority of cases to decide beyond a reasonable doubt whether the forms under study are distinct species or only distinct races. Lion, tiger, leopard, and domestic cat are species; Angora cat and alley cat are surely not species but races. However, "borderline cases," in which it is impossible to decide whether one is dealing with species or with races, do exist. Indeed, their existence was used by Darwin to demonstrate organic evolution. If species are the primordial units of creation, or else if they arise by sudden leaps (as thought by G. St. Hilaire and recently by

Goldschmidt), then we should be able to find methods to decide whether any two forms are still races or already species. If, on the other hand, species evolve gradually from races, then the decision will be possible only in some, perhaps in a majority, of cases, but at least some instances must be found in which forms are too distinct to be races but not distinct enough to be species.

RATE OF EVOLUTION

The first director of the Bishop Museum, Dr. W. T. Brigham, had so much faith in Dr. Perkins as a collector that he thought that Perkins had collected nearly all the Hawaiian insects. He used to say, jokingly perhaps, that evolution was going on at an extraordinarily rapid rate in Hawaii, because of the numerous new species which were constantly being discovered by Swezey and other workers after Perkins had finished his survey.

It is apparent that the rate of change in organisms does not follow a set pattern; it is a variable. It may be different between various groups of organisms, and it may vary in rate and intensity within groups in different places and at different times.

Evolution in the tropics should be faster than in higher latitudes because we have more generations per year in many groups. Some insects breed almost continually the year around, and several or many generations are produced each year. Likewise, our land snails reproduce almost continually.

We are confronted with extremely difficult problems when we attempt to interpret evolutionary rates, because we are only at the threshold of knowledge concerning such phenomena, and we know little about the causes and effects. From what we have observed, we may venture some remarks upon relative rates of evolution upon these islands.

The native species we see here are largely those which have developed on these islands. Hence, they are younger than the islands. But we do not know the age of any Pacific island within any but broad ranges of age estimation. Someday when more is known about the age of the land we will know more about possible evolutionary rates. There are few fossils to guide us in our work here, and those which have been found are all of late Pleistocene, or Recent age.

Perhaps the narrowest age range which could be given to an island upon which endemic species have developed would be similar to that of the elevated coral atoll of Henderson (in the Pitcairn group). This island has emerged recently and now stands somewhere near 100 feet above the sea. The endemic plants, land molluscs, insects and birds of that island have developed on it since it rose high enough above the waves to provide ecological conditions suitable for the support of such native organisms. These endemic species are younger than the island as it exists today. It is improbable that these endemic forms developed until the island had emerged for a significant distance above the waves, for none of the many neighboring atolls in the great Tuamotu Archipelago has such a distinctive endemic biota. It appears, then, that the species endemic to Henderson are recent species, and that their age is a matter of a few thousand years at most. Moreover,

at the rate natural erosion is progressing on this tiny coral island, it cannot be expected to remain at its present height for very long. It will soon be worn down to sea level again, and, unless the island rises further from the sea, its endemic terrestrial biota perhaps will suffer complete extermination before many centuries have passed.

Here, then, is a base to start on. If species could have developed in geologically very recent times on low, flat-topped Henderson Island with its plain topography and few ecological niches, then some species on other islands are equally as young.

After detailed and careful field work, one of the most astute of Hawaiian geologists has placed the subaerial age of the island of Lanai in the most recent one-fifth of the Pleistocene (Wentworth, 1925). In spite of the small amount of collecting done on Lanai, and in spite of the vast deforestation and extermination which took place before any natural history survey was made, there has been assembled a large suite of endemic species of insects, land snails, birds and plants which have evolved upon Lanai. It appears, then, that a large number of endemic organisms has been evolved on that island in less than about 130,000 to 200,000 years.

Any changes in land and in ecological or other conditions which have influenced evolution are older than the species acted upon. I wish to re-emphasize this point. Any insects which are dependent on plants as factors of speciation are younger than the plants which played the influential roles in their evolution. Unless we are grossly misled, host isolation has played an obvious, dominant role in speciation among Hawaiian insects.

The profuse speciation of *Hyposmocoma*, *Plagithmysus*, *Proterhinus* and other insect genera in Hawaii probably went hand in hand with the development of the highly diversified flora. Some groups arrived after the flora was well developed and they also speciated extensively. It is perhaps impossible to say now whether a group "grew up" with the flora or quickly adapted itself to an already diversified flora. It does not appear that any more time than the Pleistocene and Recent periods need be required for many of these specific segregates, as well as numerous genera, to have developed distinctiveness. In fact, it seems that the ages of many of these forms possibly should be measured in thousands of years, rather than the millions some workers believe requisite. Other groups are old, and their ages go back hundreds of thousands or a million or so years. When we begin to speak of "many millions" of years on mid-Pacific islands, we extend our discussions to ages before the present landscapes which have exerted such a profound influence on the development of the biota came into existence, and such long periods of time are largely irrelevant to species formation on these islands. We do take millions of years into consideration when we discuss some stem groups, certain genera and the progenitors of certain groups of our plants and animals. It appears consistent with geological history to conclude that the terrestrial biota of the Hawaiian Islands began its local development in Pliocene time and that its greatest flowering came in the Pleistocene.

It is possible to cite many examples of all extremes in species development among the Hawaiian insects. We have some forms which are so weakly differentiated as to be hardly recognizable as different entities, and forms at the other end of the line which have undergone such profound differences that they are or might be called genera.

It appears that the compactness of the area, its small geographical expanse, and easy availability of food are conducive to speciation. The small sizes of the populations and the ease of isolation contribute to the change. It is believed that isolation of small populations for even relatively short periods of time may lead to inter-colonial differences which may in turn lead to speciation. The small sizes of our insular areas are a very real aid to speeding up of the speciation processes. Moreover, these small populations are isolated from one another, and this contributes to more rapid change than would occur in wide-ranging populations.

Dr. Perkins (1913:ccviii-ccix) said:

I once examined two large series of *Nesosydne pikturi* from two different stations in the mountains behind Honolulu, where the species is very common. The first lot were taken from a number of trees, growing near together, in a rather open spot, the second lot from an isolated tree distant not many hundreds of yards from the former. Although possible individuals might have been picked from each lot agreeing exactly, yet on the whole the two series were so distinct superficially, that until I examined the genitalia I had great doubts whether those from the isolated tree were not a really distinct species. . . . In addition to this, a colony of a species infesting one tree sometimes shows considerable differences in appearance, when compared with a colony infesting another tree, even though the distance between the two is small, and these differences are likely to be increased, when colonies from more isolated spots are examined. I have little doubt that any number of superficially distinct forms could be obtained by selective breeding. It is possible that the appearance of individual colonies is often due to the nature of the original parents that colonized the tree, for colonies, if undisturbed, persist on a single tree, as I have experienced, for years.

In certain endemic species or in groups of species which appear to have been, geologically, comparatively recent immigrants, we find that there is considerable variation and it is difficult to decide whether to call the forms variants of a single species or to segregate them as varieties, subspecies or species. I am not familiar enough with birds to pass judgment, but I may call attention to the fact that the California linnet was purposely introduced to Hawaii, and that when a collection of the descendants of the original stock was made some years later, they were found to differ so much from the normal form found in California that they were made the subject of a special report by an eminent ornithologist (Grinnell, 1911). I have been told that individuals making up the Hawaiian population of an introduced Asiatic frog differ from those found in their homeland. If these differences are real, then here are examples of the beginnings of speciation.

A problem of great interest, and one which should receive careful consideration, is that of the leaf-rolling caterpillars attached to banana. These belong to the endemic genus *Omiodes*, which is an ally or segregate of *Nacoleia*. There are 23 described species in Hawaii, and others are known by their larvae only. The group has been studied carefully by Dr. Swezey for 40 years. The larvae of various

species feed on palms, grasses, sedges and on certain liliaceous and leguminaceous plants, but there are five described species which appear to be restricted to the banana. These are distinct forms, and they can be distinguished from one another in both the larval and adult stages. If our observations are correct, and if these several species are restricted to banana, and we have no reason to doubt this, then we have here an example of a species complex having arisen within about 800 years. There is no doubt that the banana was brought to Hawaii by the ancient Hawaiians who colonized Hawaii about 800 years ago. There are no bananas anywhere on the islands of the deep Pacific Basin which were not introduced by man. Hawaii was colonized by natives who sailed here from the Society Islands. Neither *Omiodes* nor *Nacoleia* is found in the Society Islands. The Hawaiian *Omiodes* form a closely interrelated, compact group of forms which appears to have originated in Hawaii following a single chance invasion. There can be no doubt that these banana-feeding species have arisen locally from other Hawaiian species. From the data at hand, then; it appears reasonable to conclude that these forms have arisen in about 800 years or less.

When evolution takes place slowly, and/or when extinction is active, many distinct genera and groups of species, frequently isolated by well-marked morphological gaps, are developed. Where speciation is rapid, great species complexes of closely allied or intergrading species in relatively few genera are developed. The Hawaiian plants, land snails and insects definitely fall in the second, or rapid, category.

It has been held by some workers that the center of greatest proliferation of species marked the place of origin of a genus. This "rule" is valueless in the majority of examples of species complexes in Hawaii. Of course, we do have genera which have evolved here and in which the development of species complexes has been entirely local; the "rule" may be applied to such genera. Hawaii probably is one of the most recently colonized places inhabited by the ground-beetle genus *Mecyclothorax*, yet there are 85 known forms in Hawaii but only about 25 in the rest of its range. It had its origin in the Australian Region. Similarly, the *Proterhinus* weevils have explosively speciated in Hawaii, and although over 180 kinds have been described in Hawaii, the genus is an immigrant. The nearly world-wide wasp genus *Odynerus* apparently originated long before the Hawaiian Islands ever felt the air, yet we have the world's greatest single complex of species in Hawaii. (It is particularly significant to this discussion that the vespoid wasps did not develop until Eocene time and that the genus *Odynerus* is much younger. It is not improbable that the more than 100 Hawaiian species are post-Pliocene in age.) The same applies to the *Nysius* bugs, to other insects, to many plants and to land Mollusca. These forms have radiated out to fill the numerous empty niches found upon these islands, and their development can only be described by saying that it has been "explosive."

One might liken some of the speciation in Hawaii to what might happen if one could develop in a laboratory a series of mutant types of *Drosophila* and could release them in a new area and have many of the mutant forms survive as distinct

entities which would set up new species because they found conditions favorable to their existence. Or, we might compare certain conditions in Hawaii with those under which we raise prize cattle, dogs, pigeons, etc., which could not for long hold their own in the wild. Some mutant forms get along here which might not stand a chance of survival on a continent.

The rate of evolution among the Hawaiian terrestrial Mollusca appears to be much more rapid than most malacologists will admit. Different rock piles and different shrubs and trees separated only by a few yards support distinguishable forms. The "colony system" of collecting (whereby each colony of shells is sampled and the material kept separate) has been found to be the soundest method of collecting because of the obvious differences between small populations. No rock pile, tree or shrub can be very old on these islands, and the population differences appearing in isolated colonies must be, at least in part, younger than their habitats. The very fact that these differences can be detected so easily is proof of rapid evolution.

It is significant that competition, predacity and parasitism are generally of low grade on islands, and these influences favor explosive types of speciation.

Perhaps it will not be out of place to call attention to Crampton's often-quoted researches (1917, 1925, 1932) on the *Partula* land snails of the Society Islands. Crampton concluded that evolution was proceeding so rapidly there that he not only found significant speciation differences between his material and that collected earlier by other workers, but he also found differences in his own material collected after an 11-year interval. I do not wish to belittle Crampton's outstanding monographs produced after years of concentrated labor, but I must take issue with the above conclusions. We collected in the islands visited by Crampton during the Mangarevan Expedition in 1934 and now feel that some of Crampton's basic data were partly incorrect. Crampton's early predecessors collected at a time when the forest came down close to the beach and when it had not retreated so far or so rapidly as it has before man in more recent times. The early collections were mostly made at low elevations near the coasts. When Crampton collected, his snails were found farther inland. His collections came from other colonies, and hence they showed population differences in his biometrical studies. Furthermore, it is possible that Crampton collected from other populations after his 11-year gap in collecting. When we visited the islands we collected higher up in the mountains and found species and forms never seen by Crampton! These things had not evolved since Crampton's time; they were simply obtained from different populations in different localities.

In almost every section of the terrestrial Hawaiian biota, or in all of it, the primitive groups are conspicuously absent. For example, the gymnosperms are wanting; the primitive orders of insects are either unrepresented or are poorly developed; among the vertebrates there are no primitive forms—the birds are evidently all Pleistocene or Recent derivatives. On the other hand, some of the malacologists are not inclined to concede that the land snails are anything but ancient. However, H. B. Baker, who has made what is generally considered to

be one of the soundest and most complete surveys of any group of Polynesian snails yet written, considers the much-speciated zonitid snails to be a comparatively modern group. He says (1941:347) that they are probably "the most advanced families of the terrestrial mollusks which have endemic species in most parts of the Pacific region." Baker also concludes (p. 360) that "their immigrations have probably been relatively recent." He recorded 266 species, 95 percent of which are endemics, from Polynesia. He found that his studies did not support the theories of certain other malacologists who have demanded large land areas of great age in the Pacific, but he emphasized the fact that the group he was working on is a recent one.

If some malacologists are correct in their conclusions that certain of the Polynesian land snails are primitive types, then it appears more plausible to assume that possibly they are derived from primitive stocks through the processes of inter-insular segregation outlined above, and that their present intense speciation is a geologically recent flowering, a resurgence of evolutionary potential. This would bring them more in line with the plants and with other animal developments of Polynesia. It is illogical to suppose that the land snails are utterly out of step with the remainder of the biota. It is of real significance that modern anatomical studies of land snails are bringing to light revolutionary new conclusions which were quite masked when the shells alone were studied. In many groups conclusions drawn from fossils or from shells alone can hardly be used for data applicable to modern studies of relationships and distribution in the light of present findings.

Because many of our groups of genera and species are highly developed, diversified and divergent, taxonomists have been led to overemphasize greatly their peculiarities rather than to emphasize their phylogenetic similarities. Thus, the true relationships of some of our groups have been masked in inaccurate taxonomy for many years. For example, the molluscan groups Achatinellidae and Amastridae have been considered endemic Hawaiian families which are without allies elsewhere, and they have been used by some workers to emphasize especially the peculiarities of Hawaii. The presence of such endemic *families* in Hawaii indicates that the islands are remnants of a great Pacific continent—so some investigators have held. However, more detailed anatomical studies by Cooke and his protégé Kondo indicate that the family Achatinellidae is a local divergent specialization from a basic stock belonging to the widespread Pacific family Tornatellinidae, which is so highly developed, diversified and widespread in eastern Polynesia. Moreover, the two subfamilies of the Amastridae appear to have been derived from two distinct stocks which perhaps will come to be considered as no more than subfamilies in association with the nearly world-wide family Pupillidae. In fact, one of these subfamilies evidently will be merged with the Holarctic Cochliopinae.

If the remarkable drepaniid birds of Hawaii have evolved and radiated to such an extreme degree and have developed such a large complex of genera and lesser forms in Pleistocene time, then is it not equally possible that our more rapidly

reproducing insect and land-snail faunas could have developed their present multiplicity of species largely since late Pliocene time?

EXTINCTION IN RECENT TIME

Before the coming of man, native forest clothed the islands from seashore to timber line as it does today in undisturbed areas of certain other Pacific islands. Isolated lowland pockets of native plants, lowland fossil beds and other evidence support this conclusion. Native animals had a similar distribution. Native drepaniid birds were found at sea level and frequented coconut trees about the native villages when Captain Cook visited the islands, but for probably more than a century these birds have been unable to live at such a low level. After the arrival of the Polynesians, apparently about the twelfth century, the rapid retreat of the forests began. Fires set by the natives, as is still being done all over the Pacific, made great advances through the lowland and dry-land forests. After Captain Cook discovered the islands in 1778 and following the subsequent introduction of cattle, goats, sheep, horses and other domesticated animals (the Hawaiians brought only the fowl, swine, dog and rat with them), and followed in turn by agricultural development by the white man, the forest retreat was alarmingly rapid. The shallow-rooted endemic plants cannot tolerate grazing. When the undergrowth is eaten away, the thin soil dries out rapidly, and, excepting for isolated trees, the forest vanishes.

Hartt and Neal (1940:251) say:

In 1793 the first cow and bull were landed on the island of Hawaii, at Kawaihae, and were released under a ten-year protective law. They increased rapidly to thousands, and in 1822 they were living in wild herds on Mauna Kea as observed by Goodrich. In 1856 they were so numerous and harmful to vegetation that Hillebrand, according to Judd, wanted them removed. In 1931 they were removed from upper Mauna Kea. Not only wild cattle but wild goats, sheep, horses, and hogs were offenders. By denuding the ground they caused the formation of erosion gulches. Horses were introduced in 1803, and wild ones lived on Mauna Kea until 1932, when they were removed from the upper slopes. Sheep were caught by wild dogs until the dogs were removed; by 1935 they had increased to 40,000. Sheep, largely, have prevented the development of *Sophora* seedlings. In 1909 the Government made upper Mauna Kea a forest reserve, which by March 1936, included 85,000 acres. In January, 1937, a fence 55.5 miles long was completed, encircling Mauna Kea between altitudes 6,000 and 8,000 feet and protecting 88,108 acres of the summit area from sheep, cattle, and hogs. In August 1935, we saw very few seedlings or young trees, but many old and dying trees.

The introduction of nematodes and plant diseases of various sorts speeded the destructive processes. Introduced grasses and other plants smother young growth and prevent the reproduction of forest seedlings. Today there are several million acres where hardly a native plant can be found. Not one-quarter of the original forest cover remains in these islands. Fortunately, however, during the last quarter of a century steps have been taken to safeguard our dwindling segments of this marvelous heritage. By legislation, by scientific planning, by fencing, by the control of feral animals and by development of forest-reserve areas, the extreme

rate at which our forests were disappearing has been decreased markedly. In fact, some forest areas are coming back slowly. But much remains to be done, and it is too late to save what has been lost. At the present time, about one-fourth of the total land area of the main Hawaiian Islands is classed as forest reserve. Not all the forest reserve is clothed in native forest, however. The conservation program has been carried on because of the realization that forest cover is essential in the preservation and protection of the most valuable mineral resource in the islands—water.

The changes wrought on the natural balance of plants and animals on these lands has been tremendous. Extermination has been extraordinary. We lost forever—before a scientist ever had an opportunity to examine the area—almost all data concerning the true character of the lowland flora and fauna. Here and there in small pockets we have found vestiges that give us a few clues. We find Recent fossil terrestrial molluscs which tell us much. But we know next to nothing regarding the prehistoric lowland insect and bird faunas. There is not an area in the world where so many birds have become extinct in so few years as has been true here. We can tabulate some of the extinct birds because we have a few specimens collected long ago, but we have no idea of the numbers—probably many hundreds—of kinds of insects which have become extinct since man appeared on the scene. There has not been an endemic insect described from the islands of Niihau or Kahoolawe. There is a remote possibility that some few still exist in nearly inaccessible cliff areas on Niihau, but the endemic plants and animals of Kahoolawe have long since been extinct. Cattle, sheep and goats ate the native vegetation off that island long ago, and for years it has been literally blowing out to sea. It is now almost divested of its soil and is uninhabited. What a pity that we know nothing of its indigenes!

If it were not for the introduction of numbers of predatory and parasitic insects, many of our endemic insects might still exist in lowland areas. The introduction of a single species of ant, the voracious *Pheidole megacephala*, alone has accounted for untold slaughter. One can find few endemic insects within the range of that scourge of native insect life. It is almost ubiquitous from the seashore to the beginnings of damp forest. Below about 2,000 feet few native insects can be found today, and those which are found there belong to a few species which form an unusual small assemblage of forms which have been able to withstand the changing environment, or have adapted themselves to new hosts.

Perkins (1903:393-394) said:

Although the destruction of the lowest belt of forest over by far the greater part of the islands has, in my opinion, been a most efficient cause of the destruction of native birds, many other causes have been at work, all of which are due to the occupation of the islands by white men. Such causes are the introduction of cattle and goats, which have extirpated or very much thinned out great portions of the native forest; of cats, foreign rats, and the mongoose (which are direct enemies), as well as the mynah, which not only attacks and drives away other birds, but also devours their eggs and young. The disturbance caused by the entrance of cattle into untrodden forest appears to be alone sufficient to scare away some species. Thus, on a very

rough lava-flow on Hawaii in 1892, the "Oo" (*Acrulocercus nobilis*) was very numerous, and as many as a dozen of these birds could be seen in a single tree, making, with hosts of the scarlet "Iiwi," the crimson "Apapane," and other birds, a picture never to be forgotten. A few years afterwards, on revisiting the spot at the same season, although the trees were, as before, one mass of flowers, hardly a single "Oo" was to be seen. The only noticeable change was that cattle were wandering over the flow and beginning to destroy the brushwood, just as they had already reduced the formerly dense forest bordering the flow to the condition of open park-land.

Cats were introduced into the Hawaiian Islands at a very early time, and, no doubt, increased excessively, while, as their owners moved from place to place, many strayed into the woods and began to feed on mice, rats, and birds. They are now found wild on all the islands, apparently only the wettest portions of the forest being free from them. On Lanai, in walking up a single ravine, I counted the remains of no less than twenty-two native birds killed by cats, and these must all have been destroyed within two days as previously the whole gulch had been washed out by a heavy flood. Two cats were actually shot on this occasion as they were devouring their prey, and several others seen, but, owing to the fact that they are extremely shy and mostly nocturnal in habits, few people who have not lived much in the woods have any idea of their numbers. The common rat is also quite at home in the forests and is decidedly arboreal in habits, feeding on fruits, land-molluscs, and no doubt on birds. The mynah, which I have myself seen devouring both young and eggs of other species, has increased prodigiously, and probably exceeds in numbers the whole of the native land-birds put together. It has greatly extended its range through the forest since 1892, and on some of the islands it is now ubiquitous.

Many favorite collecting grounds—type localities—for workers active before the turn of the century are now devoid of native plants, insects and land snails, and are cultivated or are covered by city streets and buildings. Patient, repeated search in type localities in the lower forests has failed to recover a number of species especially sought after, and many of these are certainly extinct. Even in high mountain areas where cattle have run we now have great difficulty in finding many plants and insects. In some places where we can find a steep little gulch which contains a bit of native brush which the cattle have not yet destroyed, we find new kinds of insects on rare plants. Some of these species are on the verge of extinction, and some have become extinct recently.

In Perkins' time, some species of *Odynerus* wasps were common in populations of "millions." Swezey collected nine species in Iao Valley on Maui when he first visited the valley about 35 years ago, but in more recent visits he found them to be rare. Today one must work hard to capture a small series of examples in a day's collecting. *Odynerus* feed upon certain kinds of caterpillars, and probably one of the factors influencing their decline has resulted from the wholesale slaughter of caterpillars by the immigrant and introduced caterpillar parasites. These parasites have created a profound pressure on the native caterpillars. The *Omiodes* caterpillars, a favorite food for some *Odynerus*, were once common in the mountains. Because of the new parasitism, these moths are now rarities or have not been seen for years. The ramifications of influences brought to bear by new, aggressive introductions to insular faunas are frequently appreciated by only a few workers who by chance of interest have been made aware of them. Many of the moths collected early in the century by Dr. Swezey have not been

seen for years. Time and again we bring in caterpillars from the forest and rear out not the fine adult moths but introduced foreign parasites. Three introduced continental ichneumonid wasps have by themselves played the dominant role in this great reduction or extermination. These are *Casinaria infesta* (Cresson), *Cremastus flavoorbitalis* (Cameron) and *Hyposoter exiguae* (Viereck). These are general parasites on whole series of moths, and if one moth species becomes rare, the parasites can keep up their numbers on other species. Hence, there is always an abundance of the parasites, and extermination of precinctive, small populations of particular endemic moths is quite possible. If the parasites were specific, host extinction would probably not come about because when the host became rare, the parasite would also decrease in numbers.

Perkins (1913:cxvi) found about 90 percent of the larvae of the endemic long-horn beetle *Clytarlus fragilis*, and over 90 percent of those of *Plagithmysus solitarius*, parasitized by foreign *Ischiogonus* wasps. These wasps also attack our other species of remarkable plagithmysines and probably account for the rarity of most of the species today.

Perkins (in a letter) stated that on Hawaii one year he had observed cicadellid leafhoppers "dead of some fungus disease in countless thousands in the Kona district, and in a few minutes I remember filling several pill boxes, as they stuck dead, but lifelike, on the trees. No doubt these were mostly one species. I never saw another epidemic like this, and if the fungus attacked the species indiscriminately, it would go hard with the rarer ones on such an occasion!"

Dr. Cooke has told me of an early record of a disease which attacked the now scarce native Hawaiian duck. It was said that the duck died by the thousands at Pearl Harbor.

The lowlands used to teem with certain delicate and beautiful native damselflies. After the introductions of fresh-water fishes such as top minnows, the native damselflies, whose ancestors never had to protect themselves from fishes, became scarce.

Rock (1913) held that the dry, lower forest areas of the lee sides of the islands were the richest in varieties of trees, and said that in certain of these regions a botanist could collect more different kinds of trees in a day than he could find in a week or two in the rain forest. He stated that 60 percent of all the indigenous trees in the islands could be found in the leeward dry regions. If this be true, then the amount of extermination must have been great in these regions, for most of these areas are now practically stripped of native vegetation to 2,000 to 5,000 feet or more. Limited areas of dry forest are preserved best on Hawaii, Lanai and part of Maui. These may be of great interest botanically, but they are now mostly so overrun by myriads of immigrant ants that they are largely barren of native insects. We do not have a true picture of what the magnificent dry-land fauna of these islands was. What riches might the naturalist have found when such areas as the Lualualei region of Oahu, the lee side of Kauai, western Molokai, the plain of Lanai, the vast region between the isthmus of Maui

to above the Kula and Ulupalakua regions and the wide expanses of leeward Hawaii were in their natural state! We do not know how much we have lost.

The remarkable endemic genus *Carelia*, which contains the largest of all Hawaiian land snails, consists of 29 described forms. The genus is a lowland group, and probably most of the species lived below 500 feet. Of these 29, only about 7 have ever been taken alive, and of these only 2 have been taken during the last 10 or more years. From evidence presented by beds of thousands of dead shells, it is obvious that the shells once swarmed over the lowlands.

There are a number of fine trees and shrubs which are extinct and others which are on the verge of extinction in Hawaii. Some are known from small groves or from one or two existing plants only. Unfortunately, a list of these is not available, but when one is compiled, it will be rather lengthy. Some of my friends have seen destruction by cattle of the last survivors of unique, localized, native plants when a short length of fencing could have preserved the species.

Above the lower dry mountain slopes, at elevations varying usually from 1200-3000 ft., one reaches the belt of continuous forest. Where undisturbed by man or beast, this is often so dense as to be impenetrable without cutting a pathway, or at least breaking through by force. Luxuriant growths of Ieie (*Freyinetia*) in many localities and in others wiry-stemmed ferns (*Gleichenia*) make progress difficult. The width of this forest-belt varies very greatly according to the locality and according to the destruction that has been the work of man. In some places no such forest-belt exists, in others it has been reduced to an open timbered country, covered with foreign grasses. This is the last stage preceding destruction, when the remaining trees produce their seed in vain, for the thick growth of grass prevents any young trees springing up to replace the old. We have known a forest so dense that it could be traversed only along a narrow made path, generally knee-deep in mud, to be reduced to open woodland by the ravages of cattle within a period of about fifteen years. (Perkins, 1913:xxvii.)

Rock (1913:43), speaking of the middle forest zone on Mauna Loa, said:

The *Ohia lehua* gradually passes into the *Koa* forest, if such it can still be called; for nowhere has the writer found such a pitiable sight as the *Koa* forest presents in this district at about 3000 feet up to 5000 feet elevation. Here 90 per cent of these giant *Koa* trees are dead; their huge limbs dangle in the air on pieces of fibrous strings of bark, ready to drop, if stirred by the slightest breeze. The remaining 10 per cent of the trees are in a dying condition, and in a very few years the country will be entirely denuded. Huge masses of trunks and limbs are scattered over the ground, and it is really difficult to ride through this remnant of forest. . . . Trees reach here a height of 80 feet or more. This condition is mainly due to the cattle, which have destroyed all the undershrubs and also injured the trees, which are then readily attacked by insects.

On the "great central plain" of Hawaii, Rock (1913:46) noted that

On this plain are scattered many volcanic cones, mainly composed of black cinder and covered with dense vegetation. But especially on the crater bottoms one is likely to find interesting plants which have disappeared from the open plain, where they are eagerly devoured by cattle and goats, while at the bottom of these craters they are safe from their ravages. Anyone collecting on this plain should direct his steps to all these cones, as it is here only that he can obtain things of interest.

On Maui, Rock (1913:70) found that

The forests spoken of by Hillebrand at Ulupalakua have entirely disappeared and only remnants of them can be found. *Cheirodendron Gaudichaudii* is still common, besides *Suttonia*, and *Ohia lehua*; numerous still is the araliaceous *Pterotropia dipyrrena*. The undershrub is again mainly *Rubus hawaiiensis*. The species of *Cyanea* found by Hillebrand are gone forever; and where they once reared their proud palm-like crowns toward the sky there is now only grassland, with herds of cattle and ugly Eucalypti. The writer was fortunate enough to find a specimen of the long-sought-for, gorgeous *Cyanea arborea* in that locality in a small gulch inaccessible to cattle. It was the last of its race. He scoured the country for miles searching for the handsome *Cyanea comata*, but his searches were in vain: it has vanished forever.

We know that dense forest covered the area between Makawao and Ulupalakua not so long ago, because one "used to ride through the jungle on the trail" between the two points. Other stories handed down mention horses "bogged down" in the mud on the trails in the Kula region. Today there is not a patch of native forest in the entire area, and water is so scarce in the Kula district that it must be brought by a pipe line that runs for many miles to the intake in the Olinda forest reserve on the other side of the mountain; but the draft is so great that water must be rationed on occasion and expansion of agriculture is limited.

Each native plant in Hawaii supports a lesser or greater assemblage of associated insects. Many insects are absolutely host-specific. When their hostplants become restricted in range, the range of the insects shrinks accordingly. Deforestation and extermination of various trees on our islands have accounted for the extinction of an untold number of associated insects. Some insects which were at one time abundant on certain trees back of Honolulu are now no longer found, because, for many years, we have been unable to find a specimen of their hostplants.

There are many references in earlier Hawaiian literature pertaining to the abundance of various native insects, but we cannot find these insects in such abundance today. Extinction and great reduction in numbers are very real occurrences in Hawaii. There is no way of knowing what part of the insect fauna existing in Hawaii when man arrived has been exterminated, but I believe that to say a third or more of the species are now extinct would be no exaggeration. One should not forget that the living native insects we study today are largely confined to less than one-quarter of the area once available to the fauna.

ECOLOGY

This subject has been so well covered by other workers who have had an opportunity to spend much more time than I have in the forests of the Hawaiian Islands that it is appropriate for me to refer the reader to their published works for detailed accounts. Hillebrand, Perkins, Rock and W. A. Bryan have given extensive discussions of the vegetation from which the interested person may obtain an excellent picture of local conditions in their day. Henshaw (1902) has outlined the faunal zones in relation to birds. Recent workers, such as F. X.

Williams (in his series on water insects), Hosaka (in his paper on Kipapa gulch), Ripperton and Hosaka (on vegetation zones), Usinger (in his *Nysius* paper) and Hartt and Neal, have included discussions of ecology, and these authors refer to a number of other published works. An account of the climate, prepared by S. B. Jones, is included in the Ripperton and Hosaka discussion (1942).

Any area in which one can pass within a few miles on a single mountain mass from a seaside semidesert to a rain forest receiving over 50 feet of rain in a year, or from lush, steaming tropical jungle to a perpetual, subpolar desert (mean minimum July-August temperature at 13,000 feet of 0° C. or less) where snow on occasion lies on the ground the entire year at nearly 14,000 feet, and which has such a spectacular, rugged topography clothed with dense vegetation containing about 2,000 known native higher plants making up one of the most distinctive botanical provinces of the world, cannot escape having an unusual range of ecological conditions. The remarkable thing is that so many different types of ecological niches are available in such limited areas. The proper treatment of the subject of ecology in Hawaii would require a book by itself.

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INSECTS OF HAWAII

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INSECTS OF HAWAII

A Manual of the Insects of the Hawaiian Islands, including an Enumeration of the Species and Notes on their Origin, Distribution, Hosts, Parasites, etc.

by **ELWOOD C. ZIMMERMAN**

Associate Entomologist, Experiment Station,
Hawaiian Sugar Planters' Association; Curator
of Entomology, Bernice P. Bishop Museum

VOLUME 2

APTERYGOTA TO THYSANOPTERA

INCLUSIVE

Sponsored by

BERNICE P. BISHOP MUSEUM • EXPERIMENT
STATION, HAWAIIAN SUGAR PLANTERS'
ASSOCIATION • UNIVERSITY OF HAWAII



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PREFACE TO VOLUME 2

This is the second volume of the series, *Insects of Hawaii*. It records 371 insects in the orders from the primitive Thysanura through the Thysanoptera. Some of the groups included are known inadequately, and the treatment given them here is considered preliminary. A brief survey of the text will reveal how much is yet to be done.

Reference should be made to the "Preface to the First Five Volumes" in Volume 1 for detailed discussion of this series of volumes and for general acknowledgments. In addition to those persons whose aid has been acknowledged in Volume 1, the following have contributed to this volume: The manuscript for the orders of the Apterygota was read by Harlow B. Mills, Illinois Natural History Survey; that for the Orthoptera, Dermaptera, Zoraptera and Corrodentia by A. B. Gurney, Division of Insect Identification, U. S. Bureau of Entomology and Plant Quarantine; A. E. Emerson, University of Chicago, E. M. Miller, University of Miami, and J. S. Rosa, Experiment Station, H. S. P. A., read the text on the Isoptera; J. V. Pearman, England, sent numerous notes and answered many questions pertaining to the Corrodentia; the section on Mallophaga was read by Miss Theresa Clay, England, and E. W. Stafford, Mississippi State College; J. G. Needham, Cornell University, and F. X. Williams, Experiment Station, H. S. P. A., read the Odonata text; the section on the Thysanoptera was read by F. A. Bianchi, Experiment Station, H. S. P. A., and K. Sakimura, Pineapple Research Institute, Honolulu. R. H. Van Zwaluwenburg, Experiment Station, H. S. P. A., read the entire volume in original manuscript and in proof. The illustrations for this volume, as for the other four volumes in this series, were made mostly by Frieda Abernathy, University of California; Arthur Smith, British Museum (Natural History); and W. Twigg-Smith and J. T. Yamamoto, Experiment Station, H. S. P. A. These persons have done much to make these pages more complete and accurate, and my indebtedness to each of them is great.

E.C.Z.

Honolulu, Hawaii
July, 1948

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INSECTS OF HAWAII

CHECKLIST OF THE INSECTS IN THIS VOLUME

Subclass **APTERYGOTA**

Order **THYSANURA**

Family **MACHILIDAE**

Subfamily **MEINERTELLINAE**

Genus **MACHILOIDES** Silvestri
heteropus (Silvestri)
perkinsi (Silvestri)

Family **LEPISMATIDAE**

Subfamily **LEPISMATINAE**

Genus **ACROTELSELLA** Silvestri
collaris (Fabricius)
hawaiiensis (Silvestri)

Genus **CTENOLEPISMA** Escherich
urbana Slabaugh

Subfamily **NICOLETHINAE**

Genus **NICOLETIA** Gervais
 Subgenus *Anelpistina* Silvestri
meinerti Silvestri

(Two species in two genera not identified.)

Order **DIPLURA**

Family **CAMPODEIDAE**

Genus **PLUSIOCAMPA** Silvestri
 Subgenus *Microcampa* Silvestri
perkinsi Silvestri

Genus **LEPIDOCAMPA** Oudemans
giffardii Silvestri

Family JAPYGIDAE

Subfamily PARAJAPYGINAE

Genus **PARAJAPYX** Silvestri
isabellae (Grassi)

Subfamily JAPYGINAE

Genus **JAPYX** (Haliday)
sharpi Silvestri

Order PROTURA

Species not identified

Order COLLEMBOLA

Suborder ARTHROPLEONA

Superfamily PODUROIDEA

Family ACHORUTIDAE

Subfamily ACHORUTINAE

Genus **ACHORUTES** Templeton
Subgenus **Schöttella** Schaeffer
alba (Folsom)

Genus **XENYLLA** Tullberg
alba Folsom
sensilis Folsom

Subfamily NEANURINAE

Tribe PSEUDACHORUTINI

Genus **STACHIA** Folsom
minuta Folsom

Tribe NEANURINI

Genus **PROTANURA** Börner
capitata Folsom

Genus **NEANURA** MacGillivray
citronella Carpenter

CHECKLIST

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Family ONYCHIURIDAE

Subfamily ONYCHIURINAE

Genus **ONYCHIURUS** Gervais
finetarius (Linnaeus)

Subfamily TULLBERGINAE

Genus **TULLBERGIA** Lubbock
silvicola Folsom

Superfamily ENTOMOBRYOIDEA

Family ISOTOMIDAE

Subfamily ISOTOMINAE

Genus **FOLSOMIDES** Stach
exiguus Folsom

Genus **ISOTOMODES** Axelson
denisi Folsom

Genus **FOLSOMIA** Willem
finetaria (Linnaeus)

Genus **DENISIA** Folsom
falcata Folsom

Genus **PROISOTOMA** Börner
nigromaculosa Folsom

Genus **ISOTOMURUS** Börner
palustris balteatus (Reuter)

Genus **ISOTOMA** Bourlet
minor Schaeffer
perkinsi Carpenter

Family ENTOMOBRYIDAE

Subfamily ENTOMOBRYINAE

Tribe ENTOMOBRYINI

Genus **SINELLA** Brook
caeca (Schött)

Genus **SIRA** Lubbock
jacobsoni Börner

Genus **ENTOMOBRYA** Rondani
insularis Carpenter

kalakaua Carpenter
lactea Folsom
multifasciata imminuta Folsom

Genus **LEPIDOCYRTUS** Bourlet
cyaneus Tullberg
heterophthalmus Carpenter
immaculatus Folsom
inornatus Folsom

Genus **DREPANOCYRTUS** Handschin
terrestris Folsom

Subfamily PARONELLINAE

Tribe PARONELLINI

Genus **SALINA** MacGillivray
maculata Folsom

Subfamily CYPHODERINAE

Tribe CYPHODERINI

Genus **CYPHODERUS** Nicolet
assimilis Börner

Suborder SYMPHYPLEONA

Family SMINTHURIDAE

Subfamily SMINTHURIDINAE

Tribe SMINTHURIDINI

Genus **SMINTHURIDES** Börner
Subgenus **Denisiella** Folsom and Mills
ramosus (Folsom)

Subfamily SMINTHURINAE

Tribe BOURLETIELLINI

Genus **BOURLETIELLA** Banks
insula Folsom

Subfamily DICYRTOMINAE

Genus **PTENOTHRIX** Börner
dubia Folsom

CHECKLIST

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Subclass **PTERYGOTA**

Division **EXOPTERYGOTA**

Order **ORTHOPTERA**

Suborder **CURSORIA**

Family **BLATTIDAE**

Subfamily **ECTOBIINAE**

Genus **ALLACTA** Saussure and Zehntner
similis (Saussure)

Genus **GRAPTOBLATTA** Hebard
notulata (Stål)

Subfamily **PSEUDOMOPINAE**

Genus **BLATTELLA** Caudell
germanica (Linnaeus)
lituricollis (Walker)

Genus **SYMPLOCE** Hebard
hospes (Perkins)

Genus **SUPELLA** Shelford
supellectilium (Serville)

Genus **LOBOPTERA** Brunner
dimidiatipes (Bolivar)

Subfamily **BLATTINAE**

Genus **CUTILIA** Stål
soror (Brunner)

Genus **NEOSTYLOPYGA** Shelford
rhombifolia (Stoll)

Genus **PERIPLANETA** Burmeister
americana (Linnaeus)
australasiae (Fabricius)
brunnea Burmeister

Subfamily PANCHLORINAE

Genus **LEUCOPHAEA** Brunner
maderae (Fabricius)

Genus **NAUPHOETA** Burmeister
cinerea (Olivier)

Genus **PYCNOSCELUS** Scudder
surinamensis (Linnaeus)

Genus **DIPLOPTERA** Saussure
dytiscoides (Serville)

Subfamily CORYDIINAE

Genus **EUTHYRRHAPHA** Burmeister
pacifica (Coquebert)

Genus **HOLOCOMPSA** Burmeister
fulva (Burmeister)

Suborder GRESSORIA

Family MANTIDAE

Subfamily EREMIAPHILINAE

Genus **ORTHODERA** Burmeister
ministralis (Fabricius)

Subfamily MANTINAE

Genus **TENODERA** Burmeister
angustipennis Saussure

Genus **HIERODULA** Burmeister
patellifera (Serville)

Suborder SALTATORIA

Family ACRIDIDAE

Subfamily PYRGOMORPHINAE

Genus **ATRACTOMORPHA** Saussure
ambigua Bolivar

CHECKLIST

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Subfamily CYRTACANTHACRIDINAE

Genus **OXYA** Serville
chinensis (Thunberg)

Genus **PARAIDEMONA** Brunner
mimica Scudder

Family TETTIGONIIDAE

Subfamily PHANEROPTERINAE

Genus **ELIMAEA** Stål
punctifera (Walker)

Genus **HOLOCHLORA** Stål
japonica Brunner

Subfamily COPIPHORINAE

Genus **CONOCEPHALOIDES** Perkins
remotus (Walker)

Genus **BANZA** Walker
affinis (Perkins)
brunnea (Perkins)
deplanata (Brunner)
kauaiensis (Perkins)
mauiensis (Perkins)
molokaiensis (Perkins)
nihoa Hebard
nitida nitida (Brunner)
nitida crassipes (Perkins)
parvula (Walker)
unica (Perkins)

Subfamily CONOCEPHALINAE

Genus **CONOCEPHALUS** Thunberg
saltator (Saussure)

Subfamily LISTROSCELINAE

Genus **XIPHIDIOPSIS** Redtenbacher
lita Hebard

Family GRYLLIDAE

Subfamily GRYLLOTALPINAE

Genus **GRYLLOTALPA** Latreille
africana Palisot de Beauvois

Subfamily GRYLLINAE

Genus **GRYLLODES** Saussure
sigillatus (Walker)

Genus **ACHETA** (Linnaeus)
conspersa (Schaum)
oceanica (LeGuillou)

Subfamily MYRMECOPHILINAE

Genus **MYRMECOPHILA** Latreille
americana Saussure
quadrispina Perkins

Subfamily MOGOPLISTINAE

Genus **CYCLOPTILUM** Scudder
bimaculatum (Shiraki)

Genus **CYCLOPTILOIDES** Sjöstedt
americanus (Saussure)

Subfamily TRIGONIDIINAE

Genus **PARATRIGONIDIUM** Brunner
atroferrugineum Brunner
attenuatum Perkins
crepitans Perkins
debile Perkins
exiguum Perkins
filicum Perkins
freycinetiae Perkins
grande Perkins
molokaiense Perkins
pacificum Scudder
robustum Perkins
roseum Perkins
saltator Perkins
subroseum Perkins
varians Perkins
viridescens Perkins

Genus **METIOCHE** Stål
vittaticollis (Stål)

CHECKLIST

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Subfamily ENEOPTERINAE

Tribe PROGNOTHOGRYLLINI

Genus **PROGNATHOGRYLLUS** Brunner

alatus Brunner

elongatus Perkins

inexpectatus Perkins

oahuensis Perkins

robustus Perkins

Genus **LEPTOGRYLLUS** Perkins

apicalis Perkins

cylindricus Perkins

deceptor Perkins

elongatus Perkins

forficularis (Brunner)

fusconotatus Perkins

kauaiensis Perkins

nigrolineatus Perkins

nigromaculatus Perkins

similis Perkins

simillimus Perkins

Genus **THAUMATOGRYLLUS** Perkins

variegatus Perkins

Order ISOPTERA

Family KALOTERMITIDAE

Genus **CRYPTOTERMES** Banks

brevis (Walker)

Genus **KALOTERMES** Hagen

immigrans Snyder

Genus **NEOTERMES** Holmgren

connexus Snyder

Family RHINOTERMITIDAE

Genus **COPTOTERMES** Wasmann

formosanus Shiraki

Order **EMBIOPTERA**Suborder **EUEMBIOPTERA**Family **OLIGOTOMIDAE**

Genus **OLIGOTOMA** Westwood
saundersii (Westwood)

Order **DERMAPTERA**Suborder **FORFICULINA**Family **LABIDURIDAE**Subfamily **PSALINAE**

Genus **ANISOLABIS** Fieber
eteronoma Borelli
perkinsi Burr

Genus **EUBORELLIA** Burr
annulipes (Lucas)

Subfamily **LABIDURINAE**

Genus **LABIDURA** Leach
riparia (Pallas)

Family **LABIIDAE**Subfamily **LABIINAE**

Genus **PROLABIA** Burr
arachidis (Yersin)

Genus **LABIA** Leach
curvicauda (Motschulsky)
dubronyi Hebard
pilicornis (Motschulsky)

Genus **SPHINGOLABIS** Bormans
hawaiiensis (Bormans)

Family CHELISOCHIDAE

Subfamily CHELISOCHINAE

Genus **CHELISOCHES** Scudder
morio (Fabricius)

Genus **SPARATTINA** Verhoeff
nigrorufa (Burr)

Order ZORAPTERA

Family ZOROTYPIDAE

Genus **ZOROTYPUS** Silvestri
swezeyi Caudell

Order CORRODENTIA

Family PERIENTOMIDAE

Genus **LEPIDOPSOCUS** Enderlein
costalis (Banks)
marmoratus (Banks)
unicolor (Banks)

Genus **CYPTOPHANIA** Banks
hirsuta Banks

Family PSOQUILLIDAE

Genus **PSOQUILLA** Hagen
marginipunctata Hagen

Family LIPOSCCELIDAE

Genus **LIPOSCCELIS** Motschulsky
divinatorius (Müller)

Family PACHYTROCTIDAE

Genus **PSYLLONEURA** Enderlein
williamsi Banks

Family PSOCATHROPIDAE

Genus **PSYLLIPSOCUS** Selys
minutissimus (Enderlein)

Genus **PSOCATHROPOS** Ribaga
lachlani Ribaga

Family **CAECILIIDAE**

Genus **CAECILIUS** Curtis
analis Banks

Genus **HAGENIOLA** Banks
solitaria Banks

Family **PERIPSOCIDAE**

Genus **CHAETOPSOCUS** Pearman
richardsi Pearman

Genus **ECTOPSOCUS** McLachlan
fullawayi Enderlein
hawaiiensis Enderlein
perkinsi Banks

Family **HEMIPSOCIDAE**

Genus **HEMIPSOCUS** Selys
roseus (Hagen)

Family **ELIPSOCIDAE**

Genus **KILAUELLA** Enderlein
criniger (Perkins)
debilis (Perkins)
erythrosticta (Perkins)
frigida (Perkins)
inaequifusca (Perkins)
micramaura (Perkins)
psylloides (Perkins)
vinosa (McLachlan)

Genus **PALISTREPTUS** Enderlein
inconstans (Perkins)
montanus (Perkins)

Family **PSOCIDAE**

Genus **PSOCUS** Fabricius
distinguendus Perkins

haleakalae Perkins
heterogamias Perkins
hualalai Perkins
kauaiensis Perkins
konae Perkins
lanaiensis Perkins
molokaiensis Perkins
monticola Perkins
oahuensis Perkins
simulator Perkins
sylvestris Perkins
unicus Perkins
vittipennis Perkins

Order MALLOPHAGA

Series AMBLYCERA

Family GYROPIDAE

Subfamily GYROPINAE

Genus **GYROPUS** Nitzsch
ovalis Nitzsch

Subfamily GLIRICOLINAE

Genus **GLIRICOLA** Mjoeberg
porcelli (Linnaeus)

Family BOOPIIDAE

Subfamily BOOPIINAE

Genus **HETERODOXUS** Le Souëf and Bullen
spiniger (Enderlein)

Family MENOPONIDAE

Subfamily MENOPONINAE

Genus **EOMENACANTHUS** Uchida
stramineus (Nitzsch)

Genus **MENOPON** Nitzsch
gallinae (Linnaeus)
phaeostomum Nitzsch

- Genus **MYRSIDEA** Waterston
 conspicua (Kellogg and Chapman)
 crytostigma (Kellogg and Chapman)
 invadens (Kellogg and Chapman)
- Genus **MACHAERILAEMUS** Harrison
 hawaiiensis (Kellogg and Chapman)
- Genus **COLPOCEPHALUM** Nitzsch
 brachysomum Kellogg and Chapman
 discrepans Kellogg and Chapman
 hilensis (Kellogg and Chapman)
 turbinatum Denny
- Genus **ACTORNITHOPHILUS** Ferris
 epiphanes (Kellogg and Chapman)
 kilauensis (Kellogg and Chapman)

Subfamily ANCISTRONINAE

- Genus **ANCISTRONA** Westwood
 vagelli (Fabricius)

Series ISCHNOCERA

Family TRICHODECTIDAE

- Genus **TRICHODECTES** Nitzsch
 canis (Degeer)
- Genus **BOVICOLA** Ewing
 bovis (Linnaeus)
 caprae (Gurlt)
 equi (Linnaeus)
 ovis (Linnaeus)
- Genus **FELICOLA** Ewing
 subrostrata (Nitzsch)

Family PHILOPTERIDAE

- Genus **ANOTOECUS** Cummings
 dentatus (Scopoli)
- Genus **DOCOPHOROIDES** Giglioli
 brevis (Dufour)
- Genus **SAEMUNDSSONIA** Timmerman
 conicus (Denny)
 snyderi (Kellogg and Paine)

- Genus **PHILOPTERUS** Nitzsch
 macgregori (Kellogg and Chapman)
 subflavescens (Geoffroy)
- Genus **RALLICOLA** Johnston and Harrison
 advena (Kellogg)
- Genus **QUADRACEPS** Clay and Meinertzhagen
 birostris (Giebel)
 oraria (Kellogg)
 separata (Kellogg and Kuwana)
- Genus **BRÜELIA** Kéler
 stenozone (Kellogg and Chapman)
 vulgata (Kellogg)
- Genus **PECTINOPYGUS** Mjoeberg
 Subgenus *Epifregata* Harrison
 gracilicornis (Piaget)
 Subgenus *Pectinopygus* Mjoeberg
 sulae (Rudow)
- Genus **HARRISONIELLA** Bedford
 ferox (Giebel)
- Genus **PERINEUS** Harrison
 concinus (Kellogg and Chapman)
 giganticulum (Kellogg)
- Genus **COLUMBICOLA** Ewing
 columbae (Linnaeus)
- Genus **LIPEURUS** Nitzsch
 caponis (Linnaeus)
- Genus **CUCLOTOSTASTER** Carriker
 heterographus (Nitzsch)
- Genus **OXYLIPEURUS** Mjoeberg
 polytrapezius (Burmeister)
- Genus **LAGOPOECUS** Waterston
 docophoroides (Piaget)
- Genus **GONIOCOTES** Burmeister
 chinensis Kellogg and Chapman
 hologaster Nitzsch
- Genus **GONIOIDES** Nitzsch
 dissimilis Denny
 gigas (Taschenberg)

lativentris Uchida
mammillatus Rudow

Genus **CHELOPISTES** Kéler
meleagridis (Linnaeus)

Species Incertae Sedis

Degeeriella (?) **diaprepes** (Kellogg and Chapman)
Degeeriella (?) **minhaensis** (Kellogg and Chapman)

Order ANOPLURA

Family HAEMATOPINIDAE

Subfamily HAEMATOPININAE

Genus **HAEMATOPINUS** Leach
asini (Linnaeus)
eurysternus (Nitzsch)
suis (Linnaeus)

Subfamily HOPLOPLEURINAE

Genus **POLYPLAX**^f Enderlein
spinulosa (Burmeister)
Genus **HOPLOPLEURA** Enderlein
oenomydis Ferris

Subfamily LINOGNATHINAE

Genus **LINOGNATHUS** Enderlein
africanus Kellogg and Paine
setosus (Olfers)

Family PEDICULIDAE

Subfamily PEDICULINAE

Genus **PEDICULUS** Linnaeus
humanus humanus Linnaeus
humanus capitis Degeer

Subfamily PHTHIRINAE

Genus **PHTHIRUS** Leach
pubis (Linnaeus)

Order **ODONATA**Suborder **ANISOPTERA**Superfamily **AESHNOIDEA**Family **AESHNIDAE**Subfamily **AESHNINAE**Tribe **AESHNINI**

Genus **ANAX** Leach
 junius (Drury)
 strenuus Hagen

Superfamily **LIBELLULOIDEA**Family **LIBELLULIDAE**Subfamily **LIBELLULINAE**

Genus **NESOGONIA** Kirby
 blackburni (McLachlan)

Genus **PANTALA** Hagen
 flavescens (Fabricius)

Genus **TRAMEA** Hagen
 lacerata Hagen

Suborder **ZYGOPTERA**Superfamily **COENAGRIOIDEA**Family **COENAGRIIDAE**Subfamily **COENAGRIINAE**

Genus **MEGALAGRION** McLachlan
 adytum (Perkins)
 amaurodytum amaurodytum (Perkins)
 amaurodytum fallax (Perkins)
 amaurodytum peles (Perkins)
 amaurodytum waianaeae (Perkins)
 blackburni McLachlan

calliphya calliphya (McLachlan)
calliphya microdemas (Perkins)
eudytum (Perkins)
hawaiiense (McLachlan)
heterogamias (Perkins)
jugorum (Perkins)
kauaiense (Perkins)
koelense (Blackburn)
leptodemas (Perkins)
molokaiense (Perkins)
nesiotes (Perkins)
nigrohamatum nigrohamatum (Blackburn)
nigrohamatum nigrolineatum (Perkins)
oahuense (Blackburn)
oceanicum McLachlan
oresitrophum (Perkins)
orobates (Perkins)
pacificum (McLachlan)
vagabundum (Perkins)
williamsoni (Perkins)
xanthomelas (Selys-Longchamps)

Genus **ISCHNURA** Charpentier
posita (Hagen)

Genus **ENALLAGMA** Charpentier
civile (Hagen)

Order **THYSANOPTERA**

Suborder **TERREBRANTIA**

Superfamily **AEOLOTHRIPIDEA**

Family **AEOLOTHRIPIDAE**

Subfamily **AEOLOTHRIPINAE**

Genus **AEOLOTHRIPS** Haliday
fasciatus (Linnaeus)

Superfamily **THRIPIDEA**

Family **THRIPIDAE**

Subfamily **HELIOTHRIPINAE**

Genus **HERCINOTHRIPS** Bagnall
femoralis (Reuter)

Genus **HERCOTHRIPS** Hood
fasciatus (Pergande)

Genus **HELIOTHRIPS** Haliday
haemorrhoidalis (Bouché)

Subfamily SERICOTHRIPINAE

Genus **DENDROTHRIPOIDES** Bagnall
ipomeae Bagnall

Genus **SCIRTOTHRIPS** Shull
antennatus Moulton

Genus **ANAPHOTHRIPS** Uzel
Subgenus **Chaetanaphothrips** Priesner
orchidii (Moulton)
Subgenus **Anaphothrips** Uzel
obscurus (Müller)
secticornis (Trybom)
swezeyi Moulton

Subfamily CHIROTTHIRIPINAE

Genus **CHIROTTHIRIPS** (Haliday)
fulvus Moulton
mexicanus Crawford
spiniceps Hood

Genus **APTINOTHRIPS** Haliday
rufa (Gmelin)

Genus **LIMOTHRIPS** (Haliday)
cerealium (Haliday)

Subfamily THIRIPINAE

Genus **MEROTHRIPS** Hood
hawaiiensis Moulton
morgani Hood

Genus **SELENOTHRIPS** (Karny)
rubrocinctus (Giard)

Genus **SCOLOTHRIPS** Hinds
sexmaculatus (Pergande)

Genus FRANKLINIELLA Karny**fusca** (Hinds)**sulphurea** Schmutz**williamsi** Hood**Genus ORGANOTHRIPS** Hood**bianchii** Hood**Genus LEUCOTHRIPS** Reuter**piercei** (Morgan)**Genus DOCIDOTHRIPS** Priesner**trespinus** (Moulton)**Genus BREGMATOTHRIPS** Hood**venustus** Hood**Genus TAENIOTHRIPS** Amyot and Serville**alliorum** Priesner**cyperaceae** Bianchi**frici** (Uzel)**gracilis** Moulton**hawaiiensis** (Morgan)**simplex** (Morison)**xanthius** (Williams)**Genus PLESIOTHRIPS** Hood**panicus** (Moulton)**Genus THRIPS** LinnaeusSubgenus **Microcephalothrips** (Bagnall)**abdominalis** (Crawford)Subgenus **Thrips** (Linnaeus)**nigropilosus** Uzel**saccharoni** Moulton**tabaci** Lindeman**trehernei** PriesnerSubgenus **Isoneurothrips** (Bagnall)**antennatus** (Moulton)**australis** Bagnall**carteri** (Moulton)**dubautiae** (Moulton)**fasciatus** (Moulton)**fullawayi** (Moulton)**multispinus** (Bagnall)**williamsi** (Moulton)

Suborder TUBULIFERA

Superfamily PHLAEOTHRIPOIDEA

Family PHLAEOTHRIPIDAE

- Genus **PHLAEOTHRIPS** Haliday
 claratibia Moulton
 mauiensis Moulton
- Genus **LIOTHRIPS** Uzel
 floridensis (Watson)
- Genus **POLYPOROTHRIPS** Watson
 biformis (Moulton)
- Genus **MACROPHTHALMOTHRIPS** Karny
 hawaiiensis Moulton
- Genus **NESOTHRIPS** Kirkaldy
 oahuensis Kirkaldy
- Genus **DERMOTHRIPS** Bagnall
 hawaiiensis Bagnall
- Genus **HOPLOTHRIPS** Amyot and Serville
 angusticeps (Bagnall)
 barbatus (Bagnall)
 bicolor (Bagnall)
 coprosmae Moulton
 dubius (Bagnall)
 flavipes (Bagnall)
 flavitibia Moulton
 hawaiiensis Moulton
 intermedius (Bagnall)
 lanaiensis (Bagnall)
 laticornis (Bagnall)
 mauiensis Moulton
 nigricans (Bagnall)
 ovatus (Bagnall)
 paumalui Moulton
 perkinsi (Bagnall)
 swezeyi Moulton
- Genus **AGNOSTOCHTHONA** Kirkaldy
 alienigera Kirkaldy
- Genus **ALEURODOTHRIPS** Franklin
 fasciapennis (Franklin)

- Genus **KARNYOTHRIPS** Watson
 dollicornis Bianchi
 flavipes (Jones)
 melaleuca (Bagnall)
- Genus **PODOTHRIPS** Hood
 Subgenus **Kentronothrips** (Moulton)
 lucasseni (Krüger)
- Genus **HAPLOTHRIPS** Amyot and Serville
 Subgenus **Haplothrips** Amyot and Serville
 davisi Bianchi
 fusca Moulton
 gowdeyi (Franklin)
 rosai Bianchi
 Subgenus **Hindsiana** Karny
 sakimurai Moulton
 williamsi Moulton
- Genus **RHAEBOTHRIPS** Karny
 major Bagnall
- Genus **DICERATOTHRIPS** Bagnall
 brevicornis Bagnall
- Genus **DICHAETOTHRIPS** Hood
 claripennis Moulton
 setidens (Moulton)

Superfamily UROTHRIPOIDEA

Family UROTHRIPIDAE

- Genus **CONOCEPHALOTHRIPS** Bianchi
 tricolor Bianchi
- Genus **STEPHANOTHRIPS** Trybom
 occidentalis Hood and Williams

INTRODUCTION

THE PHYLA OF ANIMALS, THE CLASSES OF TERRESTRIAL ARTHROPODS AND THE ORDERS OF INSECTS IN HAWAII

The Animal Kingdom is divided into a series of phyla. Perhaps all of the phyla are represented in Hawaii, but a few of the more obscure groups have not been recorded in literature as occurring here.

Zoologists vary in their concepts of phyla; the following list is representative of classifications proposed by various authorities.

- Protozoa: unicellular animals.
- Porifera: sponges.
- Coelenterata: corals, sea anemones, hydroids, jellyfish.
- Mesozoa: mesozoans.
- Ctenophora: comb jellies, sea walnuts.
- Platyhelminthes: flatworms, flukes, tapeworms.
- Nemertinea: ribbon worms.
- Nemathelminthes: roundworms, hookworms.
- Gordiacea: horse-hair worms.
- Acanthocephala: spiny-headed worms.
- Kinorhyncha: echinoderans.
- Trochelminthes: wheel animalcules.
- Chaetognatha: arrow worms.
- Bryozoa: moss animals.
- Brachiopoda: lamp shells.
- Phoronidea: phoronideans.
- Echinodermata: starfish, sea urchins, sea cucumbers.
- Mollusca: snails, squids, octopi.
- Annelida: segmented worms, earthworms, leeches, tube worms.
- Arthropoda: crustaceans, arachnids, centipedes, millepedes, mites, spiders, insects, etc.
- Chordata: tongue worms, tunicates, ascidians, vertebrates, etc.

The phyla in turn are divided into classes. The insects belong to the phylum Arthropoda, and it is in these animals with jointed legs that our interest lies. The arthropods are distinguished from other animals because they have segmented bodies whose exoskeletons contain chitin; some of the segments carry jointed appendages at some stage of the life history. Some arthropods frequently are referred to as insects, although they belong to distinct classes. The following key elucidates the characters whereby the insects can be differentiated from other arthropods in Hawaii:

KEY TO THE CLASSES OF ADULT TERRESTRIAL ARTHROPODS OF HAWAII

1. With more than four pairs of legs..... 2
 With two, three or four pairs of legs..... 6
- 2(1). With two pairs of antennae..... **Crustacea**.
 With only one pair of antennae..... 3
- 3(2). Antennae branched distad; minute soil- or humus-inhabiting animals with six to ten somites, nine pairs of legs and no respiratory organ system..... **Pauropoda**.
 Antennae not branched..... 4
- 4(3). Most somites apparently bearing two pairs of legs... **Diplopoda**.
 Body segments each bearing not more than one pair of legs... 5
- 5(4). Tarsal claws single; fifteen or more pairs of legs; spiracles numerous and on the pleura or dorsa of the post-cephalic somites; with a pair of well-developed six-segmented poison fangs in addition to mandibles and maxillae...
 **Chilopoda**.
 Tarsal claws paired; twelve pairs of legs; a single pair of spiracles, and these opening on the head; without poison fangs..... **Symphyla**.
- 6(1). With four pairs of legs..... 7
 With two or three pairs of legs..... 8
- 7(6). Microscopic, subterranean or aquatic arthropods lacking a respiratory organ system and without an external genital opening; legs each with several claws or specialized vesicles **Tardigrada**.
 Respiratory organ system developed, consisting of book lungs or spiracles and tracheae or both; reproductive system opening near base of abdomen; cephalothorax usually bearing two pairs of appendages, one of which is usually chelate, in addition to legs.....part of **Arachnida**.
- 8(6). With two pairs of legs; minute animals with the after-body covered with numerous microscopic, transverse folds or striae; abdomen fused to cephalothorax.....
part of **Acarina** of **Arachnida**.
 With three pairs of legs; head, thorax and abdomen distinct **Insecta**.

The phylum Arthropoda contains more species of animals than all the other phyla combined. There may be two million or more different kinds. The species are distributed from the floor of the deep oceans to high mountains, from torrid deserts to polar seas.

All the classes of terrestrial arthropods except the Onychophora and Pentastomida are represented in Hawaii. We are sure that the classes Crustacea, Diplopoda, Arachnida and Insecta contain endemic species, but the status of the members of some of the other classes is uncertain; they may all be immigrants. The insects are most easily separated from their allies because they have six legs.

Some insects are primarily wingless; insofar as we know, their ancestors never had wings. These forms are grouped together in the subclass Apterygota. How-

ever, there are certain members of the subclass Pterygota which have lost their wings secondarily, and for that reason it is essential to insert some of the orders which contain such wingless species in the Apterygota section of the following key to the orders of adult insects found in Hawaii. It is for this reason, therefore, that such orders as Hymenoptera will be found in two places in the key.

Some of the characters used in the key apply only to the Hawaiian members of a group and do not include various aberrant forms found elsewhere. The key is perhaps weak in a number of places, but it can only be improved by use and subsequent correction.

KEY TO THE ORDERS OF ADULT INSECTS OF HAWAII

1. Wings absent (including wingless forms of normally winged groups as well as typical Apterygota) 2
 Wings present, sometimes rudimentary, but never absent 21
- 2(1). With one or more pairs of ventral abdominal appendages (styli or uropods) and often one or two terminal abdominal appendages in addition to cerci and external genital appendages, although cerci may be absent (Apterygota) 3
 With at most terminal cerci and external genital appendages, never with additional ventral abdominal appendages (wingless Pterygota) 6
- 3(2). Antennae absent **Protura.**
 Antennae present 4
- 4(3). Abdomen not more than six-segmented, often, but not always, with a ventral springing organ on fourth ventrite; compound eyes absent, the eyes consisting of groups of separated simple eyes arranged in an "eye patch" **Collembola.**
 Abdomen with more than six segments, terminating either in a pair of unsegmented forceps or, more usually, with a pair of many-segmented cerci and with or without a third, median, cerciform appendage 5
- 5(4). Eyes present and body densely squamose in our species; a many-segmented, median, cercus-like caudal appendage in addition to the long, filamentous, many-segmented cerci; trophi external, not retracted into the head. **Thysanura.**
 Eyes absent; body without scales; cerci either many-segmented or forceps-like but without a median caudal filament; trophi hidden within head **Diplura.**
- 6(2). Cerci present 7
 Cerci absent 13
- 7(6). Body greatly and conspicuously compressed laterally, much higher than broad (placed here because of difficulty of identifying cerci) **Siphonaptera.**
 Not as above 8

- 8(7). Tarsi two-segmented; cerci one-segmented, not forceps-like **Zoraptera**.
Tarsi with three, four or five segments; cerci either forceps-like or two- to many-segmented 9
- 9(8). Cerci single-segmented and forceps-like wingless **Dermaptera**.
Cerci two- or more-segmented, not forceps-like 10
- 10(9). First segment of fore tarsi greatly inflated wingless **Embiopoda**.
First tarsal segment not abnormally enlarged 11
- 11(10). Tarsi four-segmented; social species living in wood or wood products wingless **Isoptera**.
Tarsi three- or five-segmented 12
- 12(11). Wood-boring social insects; bodies soft, white or pale-colored; first tarsal segment short wingless **Isoptera**.
Not wood-boring social species; bodies well-pigmented; first tarsal segment elongate some wingless **Orthoptera**.
- 13(6). Body greatly and conspicuously compressed laterally, much higher than broad; small, active, jumping ectoparasites **Siphonaptera**.
Body not laterally compressed 14
- 14(13). Body larviform, sac-like, legless, head and thorax fused, antennae and eyes absent; parasites of Hymenoptera and leafhoppers female **Strepsiptera**.
Not such degenerate insects 15
- 15(14). Tarsi one- or two-segmented, terminating in a bladder-like organ **Thysanoptera**.
Tarsi one- to five-segmented, but never terminating in a bladder-like organ, claws well-developed 16
- 16(15). Mouth parts fitted with mandibles for chewing 17
Mouth parts modified into sucking organs, often styliform and adapted for piercing 19
- 17(16). Abdomen constricted at base and joined to thorax by a narrow petiole wingless **Hymenoptera**.
Abdomen not greatly constricted at base, broadly joined to thorax 18
- 18(17). Antennae with three to five segments; ectoparasites **Mallophaga**.
Antennae with nine or more segments; not parasitic wingless **Corrodentia**.
- 19(16). Tarsi five-segmented wingless **Diptera**.
Tarsi with three or fewer segments 20
- 20(19). Mouth parts issuing from anterior end of head, retracted when not in use; small, depressed ectoparasites **Anoplura**.
Mouth parts not capable of being entirely withdrawn, usually arising from ventral side of head, usually obvious, often very long wingless **Hemiptera**.

- 21(1). With only two well-developed wings.....22
 With four wings (fore pair often modified, horny or leathery and of different consistency than hind pair).....25
- 22(21). Fore wings represented by a pair of clavate processes, hind wings well-developed**Strepsiptera.**
 Fore wings well-developed, hind wings represented by a pair of halteres, greatly reduced or absent.....23
- 23(22). Abdomen with greatly elongated caudal filaments; with but a single, forked vein in wings; minute insects (male coccids)**Hemiptera.**
 Abdomen without long caudal filaments; wings usually with complex venation 24
- 24(23). Mouth parts fitted with well-developed mandibles for biting and chewing; palpi long and conspicuous, maxillary palpi five-segmented, labial palpi three-segmented (some aberrant Hemerobiidae)**Neuroptera.**
 Mouth parts fitted for lapping, sucking or piercing; mandibles, if present, incorporated with proboscis and not obvious as mandibles; maxillary palpi, if distinguishable, not more than four-segmented, labial palpi absent..**Diptera.**
- 25(21). Abdomen terminating in two or three long, filamentous structures (cerci and median caudal filament); wings held vertically when at rest, with many cross-veins and intercalary veins, hind pair much smaller than fore pair; mouth parts vestigial; nymphs aquatic.....**Ephemeroptera.**
 Not such insects.....26
- 26(25). Mouth parts fitted for piercing and sucking or for sucking; conical, stylet-like, siphon-like or vestigial, not mandibulate 27
 Mouth parts with mandibles usually fitted for biting and chewing (developed but not used as biting or chewing organs in some Hymenoptera, however).....30
- 27(26). Tarsi terminating in a bladder-like organ; wings linear and usually with long fringes of hairs, with only one or two longitudinal veins or none.....**Thysanoptera.**
 Tarsi without such bladder-like organs; wings usually with more complex venation.....28
- 28(27). Not clothed with scales; fore wings usually, at least proximally, of a denser consistency than hind pair; proboscis not coiled**Hemiptera.**
 Wings and body densely clothed with either hairs or scales; fore and hind wings of similar texture, entirely membranous; proboscis either coiled or wanting.....29
- 29(28). Wings roughly hairy; mouth parts, except palpi, vestigial**Trichoptera.**
 Wings densely covered with scales; mouth parts usually developed into a conspicuous, coiled proboscis..**Lepidoptera.**
- 30(26). Fore wings leathery or corneous, not membranous, but of denser texture than membranous hind wings.....31
 Fore and hind wings membranous and of similar texture...33

- 31(30). Fore wings parchment-like or leathery, usually with a distinct complex of veins, but if with obscured venation, as in some Blattidae, then hind wings, as in the rest of the order, folded lengthwise like fans and never crosswise **Orthoptera.**
 Fore wings uniformly horny or leathery and normally without any venation; hind wings folded both crosswise (except in plagithmysine longicorns) and lengthwise 32
- 32(31). Cerci present and modified into conspicuous sclerotized forceps; hind wings semicircular, with peculiarly radiating veins and folds. **Dermaptera.**
 Cerci absent; hind wings without such venation. **Coleoptera.**
- 33(30). First fore-tarsal segment greatly inflated; cerci two-segmented; both pairs of wings similar. **Embiopoda.**
 First fore-tarsal segment not abnormally inflated. 34
- 34(33). Tarsi two- or three-segmented. 35
 Tarsi four- or five-segmented. 37
- 35(34). Antennae very short, inconspicuous, setaceous, not more than seven-segmented; wings with a complex reticulate arrangement of cross-veins, held either horizontal or vertical when at rest. **Odonata.**
 Antennae with nine to many segments, long and conspicuous; wings with few veins and cross-veins. 36
- 36(35). Wings folded flat over back when at rest and with a subbasal "fracture suture" at which point wings may be shed; maxillary palpi five-segmented, labial palpi three-segmented **Isoptera.**
 Wings normally held roof-like over body and without a "fracture suture"; maxillary palpi four-segmented, labial palpi one- or two-segmented. **Corrodentia.**
- 37(34). Abdomen with a conspicuous basal constriction and joined to the "thorax" by a narrow petiole; hind wings capable of being hooked to fore wings by a row of sclerotized hooks **Hymenoptera.**
 Abdomen broadly joined to thorax and without a distinct basal constriction; hind wings not hooked to fore wings. 38
- 38(37). Tarsi four-segmented; wings folded flat over back when at rest and provided with a subbasal "fracture suture," the part of the wing beyond the suture deciduous and the insects thus frequently found with only stumps of wings present **Isoptera.**
 Tarsi five-segmented; wings held roof-like over body when at rest and without a "fracture suture" **Neuroptera.**

Subclass **APTERYGOTA** (Brauer) Lang, 1889

(*a*, not; *pterygos*, wing)

Apterygogenea Brauer, 1885.

The orders of this subclass are the Thysanura, Diplura, Protura and Collembola. They can be distinguished from the adults of the orders of the Pterygota because they have one to several pairs of abdominal appendages in addition to external genitalia and cerci. They are primitively wingless creatures with little or no metamorphosis and most are cryptic in habit. The group as a whole is poorly known, but studies of some of its species have aided greatly in the interpretation of the ancestry, relationships and development of insects. With the debatable exception of the Thysanura and Diplura, the four orders are not closely allied to one another. In fact, the orders Thysanura, Collembola and Protura display such diversity in structural characters that little remains by which to associate the groups.

Members of all of the known orders of the Apterygota have been found in Hawaii, but not all of them are represented by endemic forms.

Order **THYSANURA** Latreille, 1796

(*thysanos*, tassel or fringe; *oura*, tail)

Lepismatids, Silverfish, Fishmoths, Machilids, Bristletails, Rockjumpers

This order includes primitively apterous insects of an ancient type with exposed, chewing mouth parts; filiform or moniliform, many-segmented antennae and cerci as well as a filiform, many-segmented, cerciform, median, caudal appendage; compound eyes present (except in Nicoletiinae of Lepismatidae); body densely squamose in the Hawaiian species, the scales imbricated; abdomen 11-segmented, at least some of the ventrites with lateral styli (really on the lateral plates or coxites) and usually with protrusible vesicles; tarsi three- or four-segmented, claws paired; metamorphosis incomplete, only slight changes other than size between the first instar and adult.

The group is composed of slippery, fast-running or jumping, elusive, mostly nocturnal insects of cryptic habits found in trash, litter on the forest floor, under bark, as commensals in ants' nests, under stones or in buildings, where some species (see Lepismatidae) constitute a nuisance of considerable economic importance. The species have the strange ability to regenerate the antennae and caudal appendages if these organs are broken.

Little is known concerning the species found in Hawaii. The group has been largely neglected by workers in Hawaii and considerable confusion exists in local literature pertaining to them. Only one systematic study has been made of the

Hawaiian species, and that is Silvestri's report in *Fauna Hawaiiensis* (1904). Biological studies of a "*Lepisma*" were made by Morita (1926), but the species was apparently misidentified (see notes under *Ctenolepisma*).

Too little is known concerning the Hawaiian species to enable any definite conclusions regarding the endemicity of the insects of this order to be reached at this time. In my opinion, the only species that might be endemic appear to be the two machilids. It seems improbable that any of the Lepismatidae are endemic, in spite of the fact that one has been described as *Lepisma hawaiiensis* by Silvestri. A detailed, comparative study must be made of all the Hawaiian species of the order before any concrete information can be presented. The habits of some species fit them for easy dispersal by commerce, and some have become widespread about the world.

The only record of parasites of Thysanura that has come to my attention is that of a strepsipteron on a *Lepisma* in France (see the section on Lepismatidae for details).

Fossil thysanurans are known from Oligocene and Miocene deposits.

TABULAR ANALYSIS OF THE HAWAIIAN THYSANURA

FAMILY	GENERA	ENDEMIC GENERA	NON-ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Machilidae	1	0	1	2	2	0
Lepismatidae	5	0	5	6	0	6
Totals	6	0	6	8	2	6

Percentage of endemism in native group: genera, 0 percent; species, 100 percent.

Percentage of present-day fauna native: 25 percent.

Percentage of present-day fauna adventive: 75 percent.

Average number of species per genus in native group: 2.0.

Average number of species per genus in adventive group: 1.2.

The figures in this table, and in the similar tables which follow in the remaining chapters, may be explained as follows:

1. "Percentage of endemism in native group: genera" means the percentage obtained by dividing the number of endemic genera by the total number of genera containing native (endemic and indigenous) species. The result is the percent of the total number of genera which contain native species which are endemic genera.

2. "Percentage of endemism in native group: species" means the percentage obtained by dividing the number of endemic species by the total number of endemic plus indigenous species.

3. "Percentage of present-day fauna native" is obtained by dividing the total number of endemic plus indigenous species by the total number of species recorded from the islands (endemic + indigenous + adventive).

4. "Percentage of present-day fauna adventive" is, similarly, the total number of species divided into the total of adventive species.

5. The average number of species per genus is obtained simply by dividing the total number of species in the native or adventive group by the total number of genera containing those species.

For purposes of simplification, I have combined species and lesser categories and have given them all equivalent rank. There are only about 50 subspecific names to consider, and the status of some of them is in doubt.

The two families of the order, both of which are represented in the Hawaiian fauna, may be separated as follows:

KEY TO THE FAMILIES OF THYSANURA

1. Compound eyes large, dorsally approximate or contiguous, body subcylindrical or somewhat laterally compressed rather than depressed; face narrower than base of an antenna between antennae; thorax gibbose; jumping insects (Machilids, Rockjumpers, Bristletails) **Machilidae.**
2. Compound eyes small and widely separated, situated near sides of head or absent; body dorso-ventrally depressed; face broad between antennae (excepting in Nicoletiinae); thorax not gibbose; swift-running, not jumping insects; (Lepismids, Silverfish, Fishmoths) **Lepismatidae.**

Family MACHILIDAE Grassi, 1888

Bristletails, Rockjumpers, Machilids

In Hawaii, this family includes two silvicolous species which appear to be endemic.

Compound eyes large, conspicuous, consisting of a large number of facets, occupying much of the front of the head and contiguous or approximate above; below each eye is a conspicuous, elongate organ, the two of which are called the paired ocelli; medially, toward the clypeus is another organ, of unknown function, called the single ocellus; face, between the antennae, narrower than the base of an antenna; maxillary palpi long, seven-segmented and held in such an attitude as to resemble legs; labial palpi three-segmented; antennae long, filamentous, composed of a large number of secondarily subdivided segments; mandibles composed of a single sclerite with distantly separated toothed incisor and molar areas and with a single basal articulation to the head; mid and hind coxae with styli in the Hawaiian species; tarsi three-segmented; abdominal coxites bearing styli on segments two to nine and exsertile vesicles on segments two to seven inclusive in the Hawaiian species.

The Hawaiian species may be found among trash, limbs and other material on the forest floor, under bark, in rotting stumps and logs, in dead tree-fern fronds and in bunch grass. They are walking insects which jump agilely. The conspicuously hunchbacked thorax, peculiar ocelli and the long styli, which resemble walking appendages, on abdominal segments two to nine are features which easily serve to distinguish the machilids from the silverfish.

Machilids are represented as fossils in Oligocene Baltic amber. Tillyard (1926) considered them to be probably the most primitive of insects.

Subfamily MEINERTELLINAE

This subfamily includes species which have the median ventrites of the abdomen mostly or entirely hidden and each coxite has one protrusible vesicle or none.

Genus **MACHILOIDES** Silvestri, 1905*Nesomachilus* Tillyard, 1924.

The Hawaiian members of this genus have exsertile vesicles on abdominal coxites two to seven, styli on segments two to nine, styli on the mid and hind coxae, and the paired ocelli are elongate, not triangular. The Hawaiian species were described in *Machilis*, but they cannot now be left in that genus. No information is available regarding the life histories or food habits of the Hawaiian species.

KEY TO THE HAWAIIAN SPECIES OF **MACHILOIDES**

1. Maxillary palpus of male with terminal segment elongate, awl-shaped, three terminal segments all slender and elongate, penultimate segment not much longer nor much broader than distal one; fore tibia of male enlarged, only slightly longer than broad.....**heteropus** (Silvestri).
2. Maxillary palpus of male with last three segments short and stout, penultimate segment distinctly longer and much broader than distal segment which is vaguely reniform, in any case not long and awl-shaped; fore tibia of male about twice as long as broad.....**perkinsi** (Silvestri).

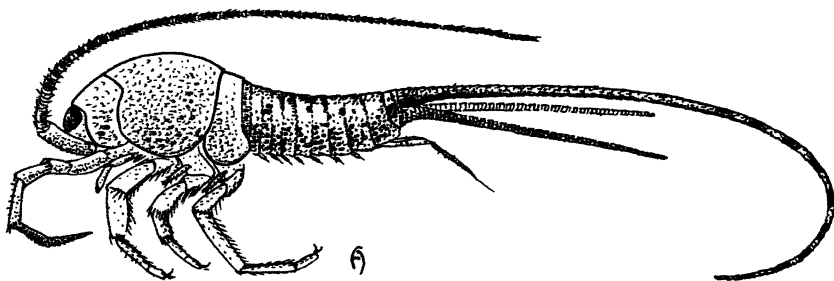


Figure 1—*Machiloides heteropus* (Silvestri). (Abernathy drawing.)

Machiloides heteropus (Silvestri), new combination (fig. 1).

Machilis heteropus Silvestri, 1904:295, pl. 8, figs. 14-16, 18.

Endemic. Kauai, Oahu, Lanai, Maui, Hawaii (no specific type locality given by author).

Habit: under dead bark, in dead tree-fern fronds, in rotting wood.

Machiloides perkinsi (Silvestri), new combination.

Machilis perkinsi Silvestri, 1904:294, pl. 8, figs. 8-13.

Endemic. Kauai (type locality: mountains behind Waimea, 4,000 feet).

Family LEPISMATIDAE (Lubbock)

Lepismidae Lubbock, 1873.

Lepismatids, Silverfish, Fishmoths

Compound eyes, if present, small, situated at the sides of the head and widely separated (absent in Nicoletiinae); ocelli absent; mandibles composed of a single sclerite with a well-sclerotized, dentate incisor area but without a distinct molar region, with two articulations with the head; maxillary palpi five- or six-segmented; labial palpi four-segmented; antennae moniliform or filamentous, very long in most species (moniliform and comparatively short only in some Nicoletiinae); coxae without styli; tarsi three- or four-segmented; some of the abdominal coxites with styli and with protrusible vesicles present or wanting.

Fossil lepismatids have been found in Miocene deposits at Florissant, Colorado, and in Oligocene Baltic amber.

The Hawaiian species are usually seen about buildings, but they are also to be found afield in trash, in bunch grass, under bark, under stones along the seashore and inland, and in the nests of some species of ants. The several species found in dwellings, factories and offices are of considerable economic importance because of the severe damage they cause to book bindings, labels, drawings, wall paper (they eat the glue between the paper and wall and cause the paper to loosen), cellophane, maps, pictures, starched clothing, pasted or glued materials, most any article made of certain kinds of paper (especially glazed and sized brands) or other materials that contain palatable starchy ingredients. They are also reported to damage linens, furs, woolens, sized silks, carpets, insect collections, farinaceous materials; rayons appear to be a favorite food of some species. Nothing is known of the food habits of our species afield. The ant-loving species are said to eat

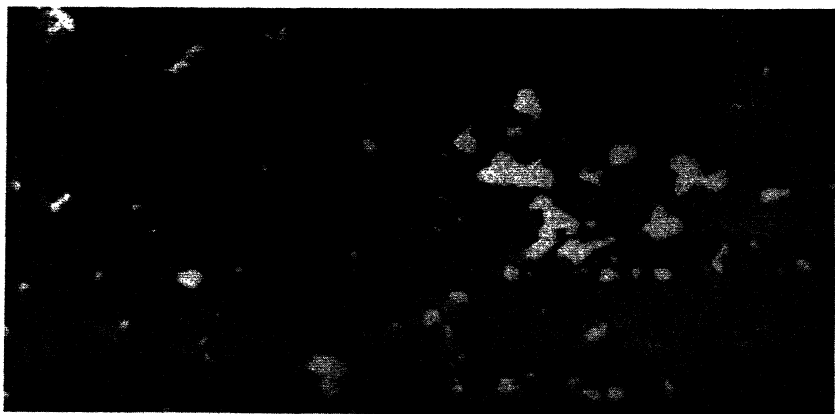


Figure 2—Part of the paper backing on a framed picture showing typical damage caused by the silverfish *Ctenolepisma urbana* Slabaugh.

regurgitated food from ants and even to excite the ants into releasing food by stroking them with their antennae. Some extra-Hawaiian species are found in termite nests (in Australia, for example).

Control: In heavily infested buildings or in rooms that can be closed tightly, cyanide fumigation is most effective and kills all stages, and if repeated at intervals of a few months, will keep damage at a minimum. Although one may kill off all individuals and their eggs in the building or room fumigated, reinfestation occurs from the gradual influx of individuals from the outside. A 5 percent solution of DDT sprayed over surfaces frequented by silverfish gives good control and is replacing the older methods, some of which are listed below.

The arsenic-flour-water pastes recommended for use in the continental United States and elsewhere have proved worthless in Hawaii. Cards painted with such mixtures have been exposed in my laboratories for several years without being touched by silverfish. An effective bait, however, is a sodium fluoride-flour mixture. I have used with success a dry mixture of three parts sodium fluoride powder to seven parts white flour, mixed well in a closed container (avoid breathing the poison) and placed in open pill boxes which are scattered around infested rooms, behind books in book cases, in drawers, in closets, under cabinets, on shelves and other places. Mallis (1944:842), who has carried on extensive silverfish poisoning tests, has found that a 5 percent sodium fluoride-95 percent flour mixture is fully as effective as higher concentrations of the poison. The bait should be replaced two or more times a year for effective control. I have found naphthalene flakes effective not only in keeping the pests away but in killing silverfish in such closed places as drawers, cupboards, closets and boxes. Paradichlorobenzene crystals can be used in the same way with excellent results. The latter substance lends itself well to home fumigation of closets and other closed places. It is more volatile than naphthalene and is a more effective fumigant. The use of cyanide fumigation one to three times a year in combination with poison baits normally will prevent serious damage. Pyrethrum powder or sodium fluosilicate dusted about infested places is recommended by some workers. Traps made from jars, bottles or glasses standing upright with tape or other rough material placed on the outside to give footing and baited with flour, glued paper or other articles known to be attacked by silverfish, are used by some people. The silverfish climb into the vessels but cannot get out because of the smooth interior glass walls of the containers. A poison to protect books from silverfish, cockroaches and Mexican book beetles is used by several libraries in Hawaii. Its formula is one ounce of white powdered corrosive sublimate and one ounce of carbolic acid crystals dissolved in one quart of ethyl alcohol. Some workers add four ounces of white shellac, which helps protect the bindings from wear. The solution is applied with a brush. It is very poisonous and is not to be used on leather.

Carpentier (1939) records the strepsipteron *Eoxenos laboulbenei* Peyerimhoff as a parasite of *Lepisma aurea* in France. The parasite also occurs in North America. This is a most unusual record of parasitism, and I am not acquainted with other parasites of silverfish.

Pemberton (1928:147) records a predaceous lepidismatid which lives in the nests and galleries of termites in British North Borneo. He says that it resembles a small *Lepisma* and that it feeds upon the eggs and nymphs of termites. An attempt was made to introduce the silverfish into Hawaii, but the culture died out before it could be released.

Lepismatids appear to enjoy a lengthy life. Individuals have been kept alive in cultures for about four years.

The tapering, roughly fish-shaped body clothed with large overlapping scales which are silvery in some species makes many of the lepidismatids slippery and difficult to pick up; hence the common name, "silverfish."

KEY TO THE SUBFAMILIES OF LEPISMATIDAE FOUND IN HAWAII

1. Eyes present **Lepismatinae.**
2. Eyes absent **Nicoletiinae.**

Subfamily LEPISMATINAE

The number of species found in Hawaii is not yet definitely known, but it is believed that several species additional to those listed are present in the Hawaiian Islands.

KEY TO THE GENERA OF LEPISMATINAE FOUND IN HAWAII

1. Caudal tergite long, V-shaped..... **Acrotelsella.**
2. Caudal tergite U-shaped, or truncate or emarginate, but never long and sharply pointed..... **Ctenolepisma.**

Genus **ACROTELSELLA** Silvestri, 1934:307

KEY TO THE SPECIES FOUND IN HAWAII

1. Dorsal scales predominantly black, but with a sharply contrasting, conspicuous band of white scales across posterior margin of pronotum; pronotum with a comb of setae between middle and each side of fore margin..... **collaris** (Fabricius).
2. Dorsal scaling brownish, without a white band on pronotum and without such combs of setae..... **hawaiiensis** (Silvestri).

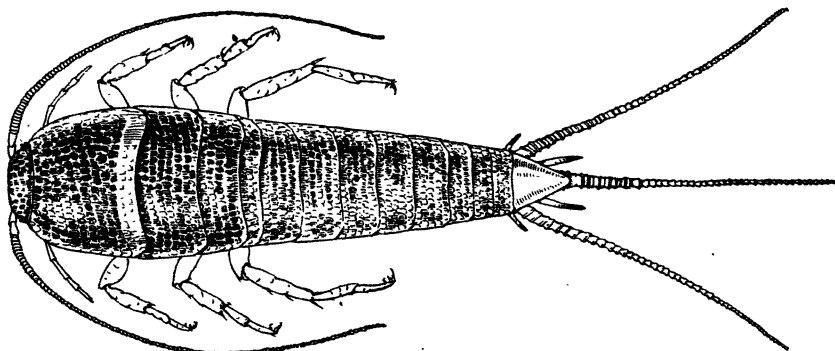


Figure 3—*Acrotelsella collaris* (Fabricius). (Abernathy drawing.)

Acrotelsella collaris (Fabricius) (fig. 3).

Lepisma collaris Fabricius, 1793:64. Sharp, 1910:185, fig. 93.

Lepisma cincta Oudemans, 1890:80.

Acrotelsa collaris (Fabricius) Escherich, 1904:107, fig. 43 *a,b*; pl. 1, fig. 3.

Oahu.

Immigrant. Described from the West Indies. Evidently widespread in the tropics; Samoa, Fiji, Java. First recorded in Hawaii by Swezey in 1925.

Under bark and in buildings.

Acrotelsella hawaiiensis (Silvestri), new combination.

Lepisma hawaiiensis Silvestri, 1904:296, pl. 8, figs. 19-27.

Kauai (type locality, 4,000 feet), Oahu, Nihoa, Necker.

Immigrant(?).

Under bark in forests; under stones near shore.

Genus CTENOLEPISMA Escherich, 1905**Ctenolepisma urbana** Slabaugh (figs. 2, 4, 5).

Ctenolepisma urbana Slabaugh, 1940:95, pl. 3, figs. 1-3, 5-6, 8, 10-12.

Oahu (and other main islands?).

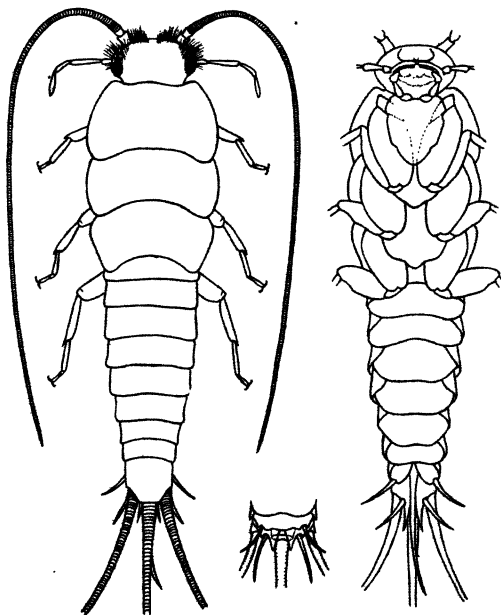


Figure 4—*Ctenolepisma urbana* Slabaugh: dorsal (left) and ventral (right) views of female to show details, vestiture removed, with an insert sketch of ventral view of apex of abdomen of male.

Immigrant. Described from Urbana, Illinois, but immigrant to North America. Long known as a common silverfish pest in buildings in Hawaii, but confused under the name *Lepisma saccharina* Linnaeus.

This is a serious pest in Hawaii, and it causes a large amount of damage. Morita's biological studies (1926) probably apply to it. For notes on control, see the preceding discussion, which was written particularly for this species. When damage is discovered, the insects causing it may often be found hiding near-by.

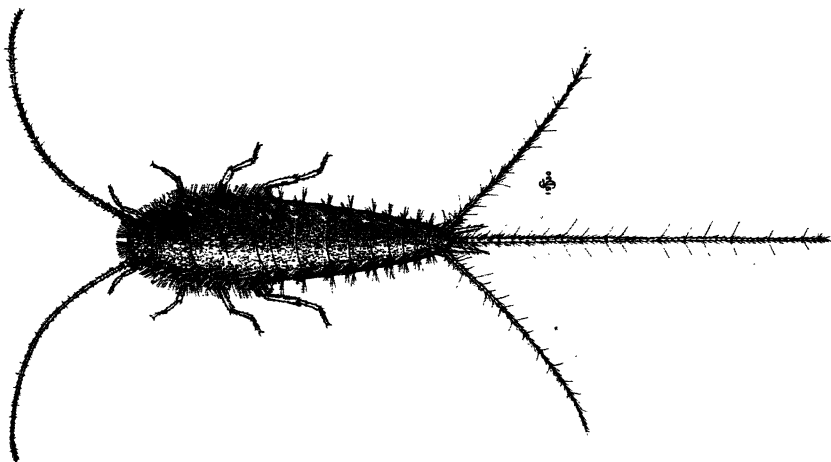


Figure 5—*Ctenolepisma urbana* Slabaugh. (From Twigg-Smith's original drawing for Williams, 1931.)

Subfamily NICOLETHINAE

Genus **NICOLETIA** Gervais, 1843

Subgenus **Anelpistina** Silvestri, 1905:111

Nicoletia (*Anelpistina*) **meinerti** Silvestri.

Nicoletia (*Anelpistina*) *meinerti* Silvestri, 1905:114, pl. 11, figs. 14-17.

Oahu.

Immigrant. Described from South America, known also from Europe and reported from the Marquesas Islands. First recorded from Hawaii by Silvestri (1912:218, fig. x) from specimens collected on Mount Tantalus in 1908.

Probably to be found in Hawaii, as in the Marquesas (see Silvestri, 1934:311), under rotting bark, in rotting banana stems and in decaying wood.

Genus(?) species(?) (fig. 6).

A small, yellow, immigrant species has been found in nests of *Pheidole megacephala* and *Tetramorium guineense* on Oahu, but it has not been determined.

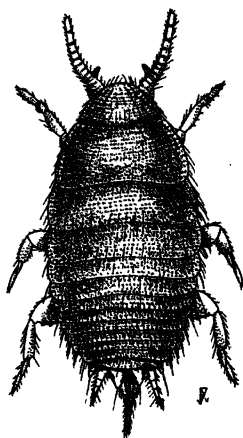


Figure 6—A small, golden-yellow, unidentified lepidid found in the nests of ants in Hawaii. (Drawing by F. X. Williams.)

Genus(?) species(?)

A small, dark, unidentified immigrant species with black scales with iridescent reflections, with a white band of scales along posterior margin of pro- and mesothorax, white patches along hind margin of metathorax, a median white patch and two lateral white patches on abdomen, has been found on desks at the Hawaiian Sugar Planters' Association Experiment Station and elsewhere in Honolulu since 1929.

The bibliography for this order is placed at the end of the Collembola section (p. 69).

Order DIPLURA Börner, 1904

(*diploos*, double; *oura*, tail)

Entotrophi Grassi, 1888.

Campodeoidea Handlirsh, 1903.

Aptera of Essig, 1942.

Campodeids, Japygids

Body squamose or not in our species; mouth parts of the chewing type, concealed in head; without eyes or ocelli; antennae many-segmented, long, filamentous; thoracic segments distinct, unusual in having three or four pairs of thoracic spiracles, abdomen 11-segmented, some of the ventrites usually with styli and protrusible vesicles; cerci either forceps-like, segmented or filiform; without a median, cerciform, caudal appendage; tarsi single-segmented, claws paired; metamorphosis slight.

This is a group of pale, blind insects of obscure habits leading a subterranean existence. They may be collected from soil and humus by flotation in water, by sifting or by the use of a Berlese funnel. Occasionally they may be found beneath logs, rocks and other objects on the ground or in decaying wood. Nothing is known regarding the life histories of the Hawaiian species.

Our knowledge of the order is insufficient to enable us to say which members of the Hawaiian group are or are not native. It appears best to assume that all of our species are immigrants. Perkins thought that *Japyx sharpi* Silvestri might be endemic, and he noted that a campodeid (*Plusiocampa perkinsi?*) was found in soil imported around plants (1913:ccxx).

I do not know of any records of insect parasites of members of this order.

TABULAR ANALYSIS OF THE HAWAIIAN DIPLURA

FAMILY	GENERA	ENDEMIC GENERA	NON-ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Campodeidae	2	0	2	2	0	2
Japygidae	2	0	2	2	0	2
Totals	4	0	4	4	0	4

Percentage of present-day fauna native: 0 percent.

Percentage of present-day fauna adventive: 100 percent.

Average number of species per genus: 1.

KEY TO THE FAMILIES OF DIPLURA FOUND IN HAWAII

1. Caudal appendages (cerci) many-segmented, long, filiform, antennae-like; without styli on first abdominal ventrite
..... **Campodeidae.**
2. Caudal appendages (cerci) single-segmented forceps; with styli on first abdominal segment..... **Japygidae.**

Family CAMPODEIDAE Westwood, 1873

Antennae with 16 to about 40 segments in our species; mandibles composed of a single sclerite with a dentate incisor area and with a single articulation with the head; palpi reduced or vestigial; abdominal ventrites two to seven with styli and protrusible vesicles; cerci eight- or nine-segmented in our species.

Campodeids are easily distinguished, pale, soil-inhabiting insects, with antennae-like cerci and mostly less than 5 mm. long.

KEY TO THE GENERA FOUND IN HAWAII

1. Antennae with less than 20 segments; body not scaled.....
..... **Plusiocampa** Silvestri.
2. Antennae with more than 30 segments; body squamose.....
..... **Lepidocampa** Oudemans.

Genus **PLUSIOCAMPA** Silvestri, 1912

Subgenus **Microcampa** Silvestri, 1934:519

Femora without dorsal macrochaetae; abdominal tergites one to seven without macrochaetae.

Plusiocampa (Microcampa) perkinsi Silvestri.

Plusiocampa (Microcampa) perkinsi Silvestri, 1934:519, figs. 1, 2. Type of subgenus.

Oahu (type locality: Honolulu).

Immigrant. Origin unknown.

Abundant in sugarcane soil.

Genus LEPIDOCAMPA Oudemans, 1890**Lepidocampa giffardii** Silvestri (fig. 7).

Lepidocampa giffardii Silvestri, 1931:282, figs. 4, 5.

Oahu, Hawaii (type locality: Hilo).

Immigrant. Origin undetermined.

Found in soil and in rotten logs.

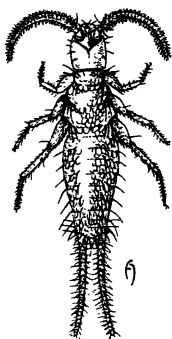


Figure 7—*Lepidocampa giffardii* Silvestri. (Abernathy drawing. Cerci broken.)

Family JAPYGIDAE Lubbock, 1873

Body without scales; antennae with a variable number of segments (38- and 18-segmented in the Hawaiian species); mandibles consisting of a single dentate sclerite with one articulation with the head; maxillary palpi reduced; labial palpi wanting in *Parajapyx*, single-segmented in *Japyx*; abdominal ventrites one to seven with styli, second ventrite only with protrusible vesicles, but with a specialized organ on either side of the first ventrite and a specialized glandular organ between these on some species; cerci heavily sclerotized forceps.

A group of blind, evidently predaceous, soil-inhabiting insects which, because of their forceps-like cerci, might easily be confused with earwigs. Our species are medium-sized insects (up to 10 mm. in length), but in Australia the largest size of any living apterygotan insect is attained by some giant members of the genus *Heterojapyx* which may be 50 mm. long.

Only two species have been recorded in Hawaii, but there are other undetermined species here. Our species may be placed in two subfamilies as follows (the number of antennal segments applies only to the two species thus far recorded from the islands and probably will have to be revised when additional species are recorded):

KEY TO THE SUBFAMILIES OF JAPYCIDAE

1. Antennae with less than 20 segments, without specialized sensory setae on any of the segments..... **Parajapyginae.**
2. Antennae with more than 30 segments, with differentiated, specialized sensory setae on segments four, five and six **Japyginae.**

Subfamily PARAJAPYGINAE

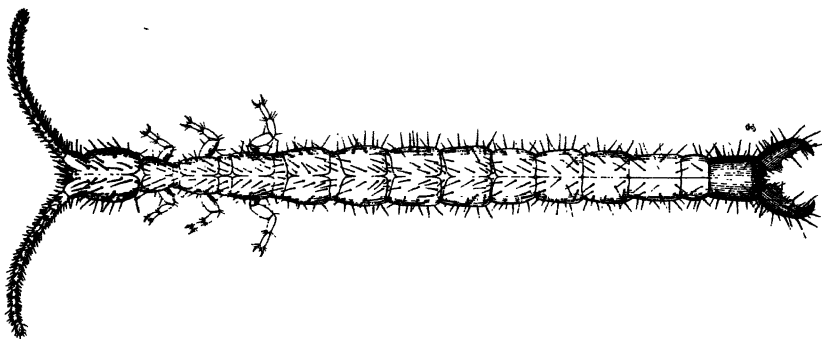
Genus **PARAJAPYX** Silvestri, 1903

Figure 8—*Parajapyx isabellae* (Grassi). (From the original drawing by Twigg-Smith for Williams, 1931.)

Parajapyx isabellae (Grassi) (fig. 8).

Japyx isabellae Grassi, 1886:1-13.

Japyx minimus Swenk, 1903:131, fig. 1.

Silvestri, 1928:79, figs. XX-XXI. Williams' (1931:351) fig. 178 is of this species.

Kauai, Oahu, Maui, Hawaii.

Immigrant. Europe (type from Sicily), China, Japan, North America. First recorded under this name from Hawaii by Van Zwaluwenburg in 1934, but known here previously as an unidentified japygid.

Abundant in soil in lowlands (from a few to over 200 individuals per square foot several inches below the surface in some places). Van Zwaluwenburg (in Williams, 1931:350) notes that this species in captivity "rasps irregular wounds in tender root cortex," but no further data on the food habits of the genus are known to me.

Subfamily JAPYGINAE

Genus **JAPYX** (Haliday)

Japyx Haliday, 1864.

Japyx sharpi Silvestri (fig. 9).

Japyx sharpi Silvestri, 1904:293, pl. 8, figs. 1-8.

Kauai (type material from Kaholuamano and Halemanu).

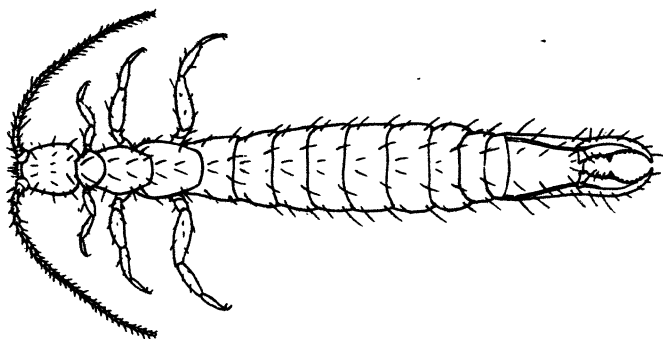


Figure 9—*Japyx sharpi* Silvestri. (Abernathy drawing.)

Immigrant. Source undetermined.

Found in rotting logs, under logs, and in soil. No study has been made of this species, and I have only one record of its capture since the type series was collected by Perkins.

The bibliography for this order is incorporated at the end of the Collembola section (p. 69).

Order **PROTURA** Silvestri, 1907

(*pro*, primitive; *oura*, tail)

Proturans

Mouth parts entognathous, of the piercing type, stylet-like; antennae absent; eyes absent; with "pseudocelli"; maxillary palpi three- or four-segmented, fitted for piercing; labial palpi two- or three-segmented; tarsi single-segmented, claws single; abdomen 12-segmented in adult, ventrites one to three with specialized sublateral appendages; cerci and caudal appendages absent; genital opening between segments 11 and 12; metamorphosis slight, consisting of the addition of three post-embryonic segments between the eighth and twelfth segments by anamorphosis.

This is a group of peculiar, minute (less than 2 mm. long), pale insects without apparent close living allies. They have been placed in a class of their own (Myrientomata) by some authors who argue that they are not insects. However, the evidence now at hand appears to support the contention that they are primitive, aberrant insects.

The Hawaiian material has not yet been identified. Van Zwaluwenburg collected the first specimens found in the islands in soil from sugarcane fields near Honolulu in 1933. He has subsequently found them in soil at different localities up to elevations of 1,000 feet on Oahu.

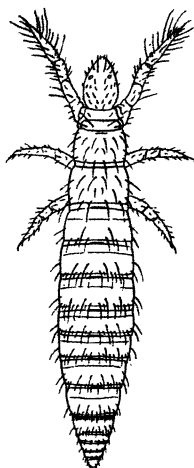


Figure 10—A typical proturan, *Acerentulus barberi barberi* Ewing. (Redrawn from Ewing, 1940:497. This species is not known to occur in Hawaii, but, because no local material is available, the drawing of the American species is used here to illustrate the Protura.)

The families are separated by Ewing (1940:517) as follows:

1. Tracheae present, opening through two pairs of spiracles, one on mesothorax and one on metathorax; all vestigial abdominal appendages two-segmented **Eosentomidae.**
2. Tracheae and spiracles absent; third vestigial abdominal appendages single-segmented **Acerentomidae.**

Ewing's paper (1940) should be consulted by anyone wishing to work on this group, for it gives methods of collecting and preservation as well as a general discussion of the order.

The literature on this chapter is included in the bibliography at the end of the Collembola section (p. 69).

Order COLLEMBOLA Lubbock, 1873

(*colla*, glue; *embolon*, a bar—referring to the ventral “adhesive” organs)

Collembolans, Springtails

Small to minute, soft-bodied, jumping insects mostly less than 5 mm. long; body variform, setose or squamose; head with entognathous mouth parts; labrum and clypeus present; mandibles present or absent—if present, slender or styliform, fitted for piercing and sucking or for chewing and then with incisor and usually

molar areas; maxillae with specialized dentate apex or styloform; maxillary palpi reduced or vestigial; labrum greatly reduced, labial palpi absent in adults; antennae four- to six-segmented, length variable, shorter than head to longer than body; compound eyes absent; with or without a group of ocelli at sides of head behind antennae, with a maximum number of eight ocelli in a group; most forms with a specialized sensory structure, the *postantennal organ*, situated behind each antenna; thorax variform, with segmentation distinct or ankylosed, or with prothorax much reduced, its notum obscure, the other segments distinct; legs evidently without tarsi, tibiae (tibio-tarsi) terminating in one or two claws (when two are present, they oppose vertically instead of horizontally); abdomen with not more than six segments, some or all of the segments ankylosed in some forms; first ventrite with a median bilobed organ, the *ventral tube*, containing protrusible vesicles; third ventrite usually with a bipartite median appendage, the catch or *tenaculum* (*retinaculum*), on which the furcula is held when at rest; fourth ventrite, on most forms, bearing the leaping organ, or *furcula*, composed of a pair of organs fused basad to form the *manubrium*, bifurcate distad to form a pair of *dentes* each terminating in a small *mucro*; cerci absent; genital opening on the caudal edge of the fifth ventrite, without external genitalia; metamorphosis slight.

Some authorities believe that the Collembola are not true insects and that they have had an independent origin from a pre-insect type of arthropod.

Springtails are among the most widespread of all insects, and are found throughout the world from north to south polar regions. They are hydrophiles found most everywhere in damp situations from ocean beach to mountain top, in soil, caves, tunnels, graves, under stones and logs, in ground surface litter, in moss and lichens, under bark, in rotting wood, in shrubbery, high up in trees, and some species are even found in great numbers on the surface of snow and on bodies of water; some are termitophiles and others myrmecophiles.

The food habits vary, some are carnivores or scavengers; others are phytophagous and feed on living and dead plant material; some are fungivorous. They are among the most important organisms in returning dead vegetable matter to the soil. Among the phytophagous species, some are of considerable economic importance in certain regions. *Sminthurus viridis*, the "lucerne flea" of Australia, for example, has received much attention because of the great damage it does to leguminous and other plants, and a large body of literature has been built up about its habits. It is considered by some workers as probably the most serious insect pest of pastures in parts of Australia where, according to Womersley (1939), infestations may run as high as 6,000 individuals per square foot of pasture. It feeds on the leaves of such plants as alfalfa (lucerne) and causes severe skeletonization. An interesting research report on the serious damage done to mangold seedlings by *Bourletiella hortensis* in England is that by Davies (1926:159). We have at least one species of the same genus in Hawaii. At least one of the species found in Hawaii (*Isotomodes denisi* Folsom) has been estimated to total more than one hundred million individuals to the acre. This same insect has been shown to cause damage to the rootlets of sugarcane by gnawing small holes in them, thus

retarding root growth with a subsequent detrimental stunting effect on the cane (Van Zwaluwenburg, in Williams, 1931:348). However, it was demonstrated experimentally that the insects are principally humus feeders and damage to the cane is negligible in soils containing a large amount of decaying organic matter. Sugarcane seedlings in flats containing little humus are likely to be attacked. Williams (1931:49) recommends pyrethrum at the concentration of 1 part per 200 parts of water as a satisfactory control spray. Only on rare occasions have these insects caused serious damage to Hawaiian crops. On Oahu, collembolans have been seen piled up in great masses in windrows along the edges of rows of pineapples. Womersley (1939:276) gives a list of all the species recorded as injurious to crops up to 1939; the list contains 69 names.

At least one species has been utilized by man. That species is *Achorutes* (*Hypogastrura*) *viatica* (Tullberg), which is used in England for cleaning the filters of sewage disposal plants.

Numerous predators such as ants and spiders are known to attack Collembola. In Australia a mite has aided in the control of the "lucerne flea" (an alfalfa pest). However, no arthropod parasites are known to attack these primitive insects.

Fossil Collembola are known from Cretaceous Canadian amber, which has disclosed the peculiar family Protentomobryidae, and from Oligocene Baltic amber, from which representatives of the families Poduridae and Sminthuridae have been described. Fossilization of such delicate, soft-bodied organisms is of rare occurrence. Tillyard described what he considered to be Collembola from Scottish Devonian deposits, but later workers appear not to have accepted his conclusions. However, Hirst and Maulik have described a species from Middle Devonian Scottish deposits which is said not to differ from living forms, but there is still a question of their true identity.

Because the Collembola as a whole are such an incompletely known group, it is not possible at this time to assign any of the species found in Hawaii to the endemic Hawaiian fauna. More than 20 species and two genera have been described from Hawaii, but with the great ease that species of this order are carried about the world by commerce, we cannot be sure that any of these species are other than immigrants which may ultimately be found indigenous to other geographical regions. None of the Hawaiian species appears to be so peculiar or so unusually isolated as to indicate probable endemism. Also, there has not yet been found in the islands a species complex of Collembola which can be compared with other such endemic groups which are so characteristic of most of the endemic Hawaiian insects of other orders. In spite of the apparent absence of the order from the native fauna, the group is a dominant one in Hawaii, and individuals may be found almost everywhere in the islands. Often, as this book was being written, trade winds have blown small species through the open window and onto my desk. Further detailed study and careful collecting in the forests may, however, reveal endemic species, since no obvious reason is seen for the complete exclusion of the order from the endemic fauna. Insofar as I know, the life history of none of the species has been studied in detail in Hawaii.

TABULAR ANALYSIS OF HAWAIIAN COLLEMBOLA

FAMILY	GENERA	ENDEMIC GENERA	NON-ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Achorutidae	5	0	5	6	0(1?)	6(5?)
Onychiuridae	2	0	2	2	0	2
Isotomidae	7	0	7	8	0(1?)	8(7?)
Entomobryidae	7	0	7	13	0(3?)	13(10?)
Sminthuridae	3	0	3	3	0	3
Totals	24	0	24	32	0(5?)	32(27?)

Percentage of present-day fauna native: 0 percent (or 15.6 percent ?).

Percentage of present-day fauna adventive: 100 percent (or 84.4 percent ?).

Average number of species per genus: 1.3.

Our knowledge of the Collembola from a world-wide standpoint is still too meager to enable us to ascertain whether or not any of the species, which from their habit might possibly be native, are or are not indigenes. Five species fall in this "possibly native" category.

Two taxonomic papers constitute the literature pertaining to the species described from Hawaii. These are Carpenter's report in *Fauna Hawaiiensis* in 1904 and Folsom's revision in 1932. We are fortunate in having Folsom's carefully written revision as a background for further work. For most of the generic and specific categories, I have followed Folsom's report, and most of the keys contained hereinafter are abstracted, reworded or revised from Folsom's originals, and to him belongs the credit for them. However, for the suprageneric classification, I have followed the more recent work of Womersley (1939) which differs somewhat from that of Folsom, and I have incorporated some of his key material in the generic and suprageneric keys. We were fortunate in having Folsom's original drawings preserved in Honolulu, and I have rearranged these and reproduced them here. Except for a couple of my sketches, the illustrations used here are from Folsom's report, unless otherwise indicated.

There are many more species of Collembola in Hawaii than those listed hereinafter—perhaps only a lesser fraction of the species now present in the islands has been recorded—and when more of them are described or identified, modifications of the keys will be required.

In spite of the small size and cryptic habits of most of the species, many are beautifully colored and peculiar in shape and structure.

KEY TO THE SUBORDERS OF COLLEMBOLA

1. Abdomen elongate, subcylindrical, segmentation distinct, thorax and abdomen not fused; elongate insects.....**Arthropleona.**
2. Abdomen conspicuously globular or inflated, not obviously segmented, the segments fused, their sutures obliterated or obscure, thorax and first four abdominal segments fused; subglobose insects.....**Symphyleona.**

Suborder ARTHROPLEONA Börner, 1901

KEY TO THE SUPERFAMILIES

1. Prothorax distinct and visible from above, well-developed, with a distinct tergum and with dorsal setae; furcula, when present, arising from fourth ventrite; antennae short, usually shorter than length of head, four-segmented; derm granular or tuberculate, not squamose.....**Poduroidea.**
2. Prothorax very small, hidden from above, without a distinct tergum, without dorsal setae; furcula, when present, apparently arising from fifth ventrite (actually arising from fourth); antennae four- to six-segmented, often longer than head and thorax; derm smooth, hirsute or squamose.....**Entomobryoidea.**

Superfamily PODUROIDEA Womersley, 1939

KEY TO THE FAMILIES FOUND IN HAWAII

1. Tergites of thorax and abdomen without pseudocelli...**Achorutidae.**
2. Tergites of thorax and abdomen with pseudocelli...**Onychiuridae.**

Family ACHORUTIDAE

Hypogastruridae Börner, 1913

KEY TO THE SUBFAMILIES

1. Mouth parts not projecting in a cone; mandibles with a molar area.....**Achorutinae.**
2. Mouth parts projecting into a cone in most genera; mandibles without a molar area.....**Neanurinae.**

Subfamily ACHORUTINAE Börner, 1901

KEY TO THE GENERA FOUND IN HAWAII

1. Postantennal organs present; eight ocelli on each side; furcula well-developed.....**Achorutes** subgenus **Schöttella** Schaeffer.
2. Postantennal organs absent; five ocelli on each side; furcula reduced, dens and mucro not or feebly separated.....**Xenylla** Tullberg.

Genus ACHORUTES Templeton, 1835

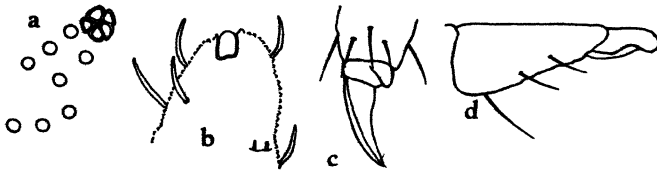
Hypogastrura Bourlet, 1839

Figure 11—*Achorutes* (*Schöttella*) *alba* (Folsom): a, eyes and postantennal organ of right side; b, dorsal aspect of apex of right antenna; c, right hind foot; d, right dens and mucro.

Subgenus *Schöttella* Schaeffer, 1897**Achorutes** (*Schöttella*) **alba** (Folsom) (fig. 11, a-d).*Schöttella alba* Folsom, 1932:54, pl. 1, figs. 1-4.

Oahu (type locality: Honolulu).

Immigrant.

In soil about pineapple roots.

Genus **XENYLLA** Tullberg, 1869

KEY TO THE SPECIES FOUND IN HAWAII

1. White species; unguis simple; sensory organ of third antennal segment without papillae between the horn-like processes **alba** Folsom.
2. Body mottled with blue above; unguis dentate; sensory organ of third antennal segment with a pair of clavate papilla-like organs between two horn-like processes **sensilis** Folsom.

Xenylla alba Folsom (fig. 12, a-g).*Xenylla alba* Folsom, 1932:54, pl. 2, figs. 14-20.

Oahu (type locality: Honolulu).

Immigrant.

In soil of pineapple fields.

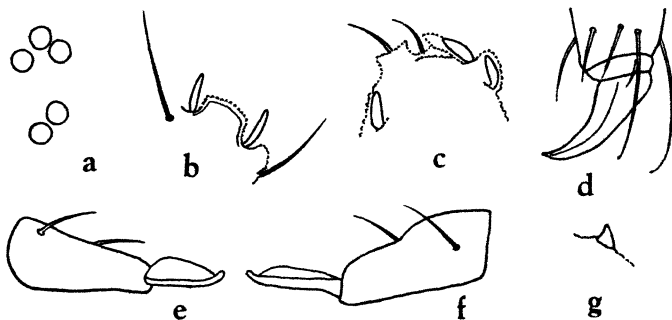


Figure 12—*Xenylla alba* Folsom: a, right eyes; b, antennal sense organ of right third antennal segment; c, dorsal aspect of apex of right antenna; d, right hind foot; e, left dens and mucro; f, right dens and mucro; g, anal spine.

Xenylla sensilis Folsom (fig. 13, a-i).*Xenylla sensilis* Folsom, 1932:54, pl. 1, figs. 5-13.

Oahu (type locality: Honolulu).

Immigrant.

In soil of pineapple fields.

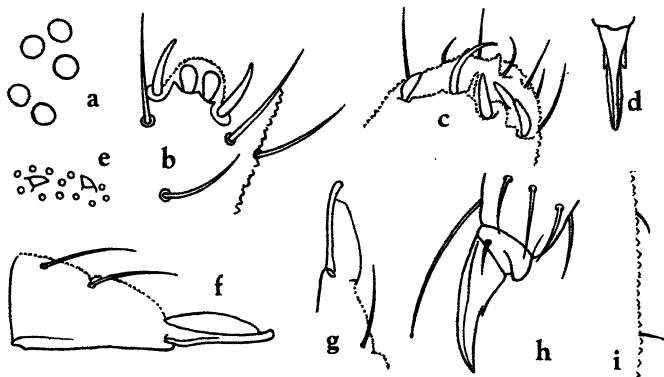


Figure 13—*Xenylla sensilis* Folsom: a, left eyes; b, sense organ of third antennal segment of right side; c, apex of right antenna, dorsal aspect; d, concave aspect of unguis; e, anal spines; f, left dens and mucro; g, right mucro; h, right fore foot; i, dorsal setae of metanotum.

Subfamily NEANURINAE Börner, 1901

KEY TO THE TRIBES

1. Body without segmental tubercles; anal segment comparatively small; supra-anal valve rounded, not bilobed... **Pseudachorutini.**
2. Body with large segmental tubercles; anal segment comparatively large; supra-anal valve bilobed..... **Neanurini.**

Tribe PSEUDACHORUTINI Börner, 1906

Genus **STACHIA** Folsom, 1932:55

Stachia minuta Folsom (fig. 14, a-j).

Stachia minuta Folsom, 1932:55, pl. 2, figs. 21–26; pl. 3, figs. 27–30. Genotype. Oahu (type locality).

Immigrant.

Widespread in soil in pineapple and sugarcane fields and lower forests.

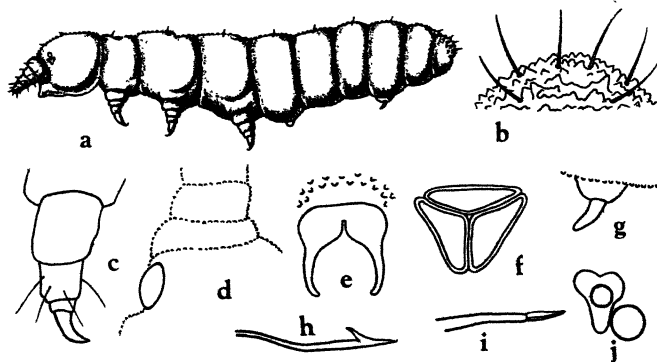


Figure 14—*Stachia minuta* Folsom: a, lateral view; b, anal segment, dorsal aspect; c, end of left fore foot; d, left eye and base of antenna; e, furcula, dorsal aspect; f, suranal and subanal valves; g, furcula, left aspect; h, mandible; i, maxilla; j, left eye and postantennal organ.

Tribe NEANURINI Börner

KEY TO THE GENERA FOUND IN HAWAII

1. Head of maxilla with toothed lamellae; ocelli and postantennal organs absent in our species.....**Protanura** Börner.
2. Head of maxilla stylet-like, without lamellae or teeth; ocelli present and postantennal organs present but reduced in our species**Neanura** MacGillivray.

Genus **PROTANURA** Börner, 1906

Protanura capitata Folsom (fig. 15, a-f).

Protanura capitata Folsom, 1932:56, pl. 3, figs. 31-36.

Oahu (type locality: Honolulu).

Immigrant.

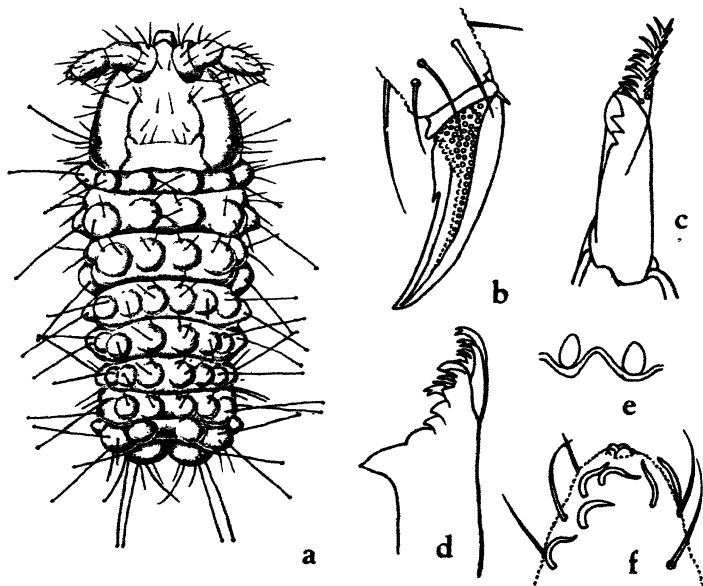


Figure 15—*Protanura capitata* Folsom: a, dorsal aspect; b, left hind foot; c, head of right maxilla; d, head of right mandible; e, sense organ of third antennal segment of right side; f, dorsal aspect of end of right antenna.

Genus **NEANURA** MacGillivray, 1893

Neanura citronella Carpenter.

Neanura citronella Carpenter, 1904:303, pl. 9, figs. 20-27.

Oahu, Maui (no more specific type locality given).

Immigrant(?).

Beneath bark of *Acacia koa*, *Gunnera*.

Family ONYCHIURIDAE Lubbock, 1867

KEY TO THE SUBFAMILIES

1. Body stout; head broad; postantennal organ in our species with less than 20 tubercles, which are branched; large sensory clubs of organ of third antennal segment smooth or tuberculate, but not bending toward each other..... **Onychiurinae**.
2. Body slender; head narrow; postantennal organ in our species with about 60 tubercles; large sensory clubs of organ of third antennal segment smooth, bent toward each other... **Tullberginae**.

Subfamily ONYCHIURINAE Bagnall, 1935

Genus **ONYCHIURUS** Gervais, 1841**Onychiurus fimetarius** (Linnaeus) (fig. 16, a-f).*Podura fimetaria* Linnaeus, 1758:609.

Lubbock, 1873:191, pl. 47. See Folsom, 1917:649, pl. 69, fig. 9; pl. 77, figs. 83-86; pl. 78, figs. 87-88, for detailed synonymy and description.

Hawaii.

Immigrant. Cosmopolitan. First recorded in Hawaii by Folsom (1932:57).

In sugarcane fields; probably common also in humus, piles of leaves, under bark and logs and in other situations.

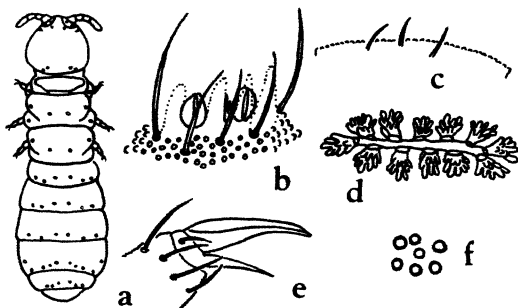


Figure 16—Details of *Onychiurus fimetarius* (Linnaeus); a, dorsal aspect; b, left antennal sense organ; c, vestiture on median line of first abdominal segment; d, right postantennal organ; e, right hind foot; f, cuticular tubercles of head. (Redrawn from Folsom, 1917.)

Subfamily TULLBERGINAE Bagnall, 1935

Genus **TULLBERGIA** Lubbock, 1876**Tullbergia silvicola** Folsom (fig. 17, a-e).*Tullbergia silvicola* Folsom, 1932:57, pl. 4, figs. 37-41.

Oahu (type from Mount Tantalus, 1,700 feet).

Immigrant.

In soil in lower forest.

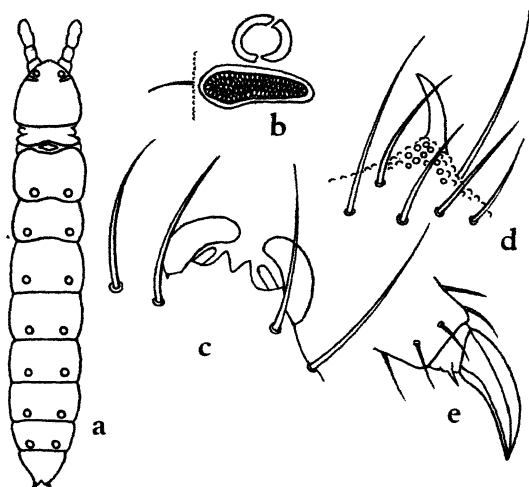


Figure 17—*Tullbergia silvicola* Folsom: a, dorsal aspect; b, left postantennal organ and pseudocellus; c, sense organ of third antennal segment of right side; d, left anal spine; e, left hind foot.

Superfamily ENTOMOBRYOIDEA Womersley, 1939

Entomobryomorpha Börner, 1913

KEY TO THE FAMILIES FOUND IN HAWAII

1. Postantennal organs present in all of our species except *Isotoma minor*; fourth abdominal segment not much longer than third; inner margin of unguis simple, not split into two lamellae; squamae never present; body setae simple or at most plumose on one side only; hind coxae without a specialized setose area **Isotomidae.**
2. Postantennal organs absent; fourth abdominal segment much longer than third; inner margin of unguis split or proximally grooved; squamae present or absent; body setae of various types but including some plumose or ciliated on all sides; hind coxae with a specialized setose or hirsute area . . . **Entomobryidae.**

Family ISOTOMIDAE Schaeffer, 1896

Subfamily ISOTOMINAE Schaeffer, 1898

KEY TO THE GENERA FOUND IN HAWAII

1. Body cylindrical, greatly elongate; prothorax elongate 2
- Body not greatly elongate; prothorax more or less reduced . . . 3
- 2(1). Derm granulate; all abdominal segments distinct, terminal ones not fused; manubrial hooks not strongly developed; one or two ocelli on each side **Folsomides** Stach.
- Derm smooth; abdominal segments four to six fused or at least with segment six shortened and modified; manubrial hooks strongly developed; ocelli absent . . **Isotomodes** Axelson.

- 3(1). Eyes reduced in number or absent; caudal three abdominal segments fused into a single mass; body pigmentation weak or wanting..... 4
 Usually with 16 eyes; three terminal abdominal segments not fused; body pigmentation usually well-developed..... 5
- 4(3). Mucro bidentate; fourth antennal segment without sensory clavae; postantennal organs present..... **Folsomia** Willem.
 Mucro falciform; fourth antennal segment with five or six large, sensory clavae; postantennal organs absent..... **Denisia** Folsom.
- 5(3). Third abdominal tergite shorter than fourth, not prolonged ventrolaterally caudad; furcula not reaching ventral tube..... **Proisotoma** Börner.
 Third abdominal tergite longer than fourth, ventrolaterally prolonged caudad; furcula reaching ventral tube..... 6
- 6(5). Mucrones lamellate; abdomen with fringed bothriotrichia..... **Isotomurus** Börner.
 Mucrones not lamellate; abdomen without bothriotrichia..... **Isotoma** Bourlet.

Genus **FOLSOMIDES** Stach, 1922

Folsomides exiguus Folsom (fig. 18, a-f).

Folsomides exiguus Folsom, 1932:58, pl. 4, figs. 42-47.

Oahu (type locality).

Immigrant.

In soil in sugarcane fields, rice fields and lower forest.

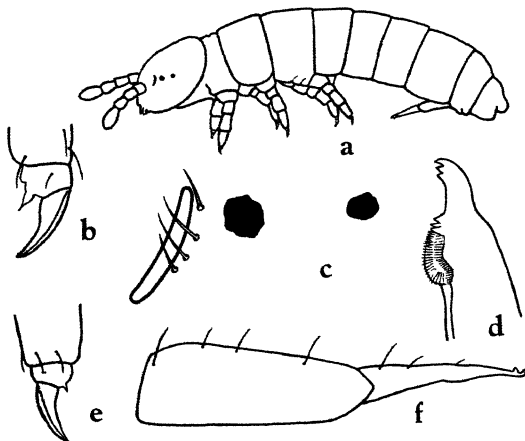


Figure 18—Details of *Folsomides exiguus* Folsom: a, lateral aspect; b, left hind foot; c, eyes and postantennal organ of left side; d, mandible; e, right fore foot; f, left aspect of manubrium and mucrodens.

Genus **ISOTOMODES** Axelson, 1907**Isotomodes denisi** Folsom (fig. 19, a-i).*Isotomodes denisi* Folsom, 1932:59, pl. 5, figs. 48-56.

Oahu, Hawaii (no specific type locality given).

Immigrant.

In soil of sugarcane fields and lower forest.

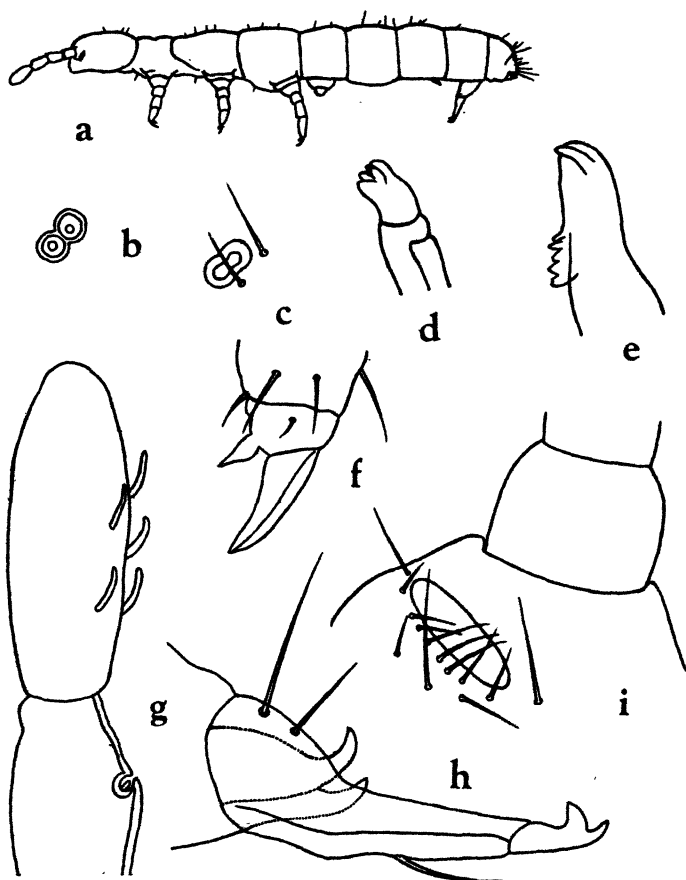


Figure 19—Details of *Isotomodes denisi* Folsom: a, lateral aspect; b, sense organ of third antennal segment of left side in optical cross section; c, the same, surface aspect; d, head of maxilla; e, head of mandible; f, left hind foot; g, ventral aspect of extremity of left antenna; h, left dens and mucro; i, left postantennal organ and base of antenna.

Genus **FOLSOMIA** Willem, 1902**Folsomia fimetaria** (Linnaeus).

Podura fimetaria Linnaeus, 1761:474. See Folsom, 1902:92, pl. 7, figs. 37-39, for re-description and synonymy.

Hawaii.

Immigrant. Cosmopolitan. First recorded in Hawaii by Folsom (1932:60).

In sugarcane soil.

Recorded elsewhere as causing serious injury to plant rootlets (Womersley, 1939:145). A common species elsewhere in soil, humus, potted plants, under logs and in similar conditions and probably with the same habits in Hawaii.

Genus **DENISIA** Folsom, 1932:61

Womersley (1939:137) includes this genus with *Folsomina* Denis.

Denisia falcata Folsom (fig. 20, a-f).

Denisia falcata Folsom, 1932:61, pl. 5, fig. 57; pl. 6, figs. 58-62. Genotype.

Oahu (type locality: Honolulu).

Immigrant.

In sugarcane soil and in debris from nest of the ground-dwelling termite, *Coptotermes formosanus* Shiraki.

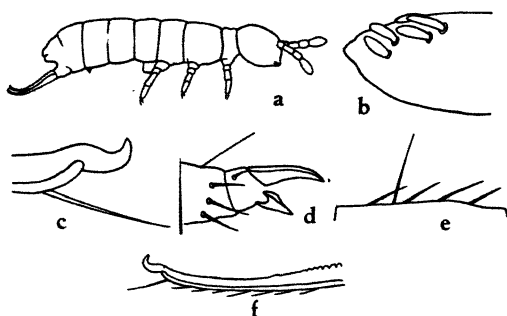


Figure 20—Details of *Denisia falcata* Folsom: a, lateral aspect; b, lateral aspect of extremity of left antenna; c, left mucro; d, left hind foot; e, vestiture on second abdominal segment; f, right mucro and part of dens.

Genus **PROISOTOMA** Börner, 1906**Proisotoma nigromaculosa** Folsom (fig. 21, a-d).

Proisotoma nigromaculosa Folsom, 1932:62, pl. 6, figs. 63-66.

Oahu (type locality).

Immigrant.

In soil of sugarcane and rice fields.

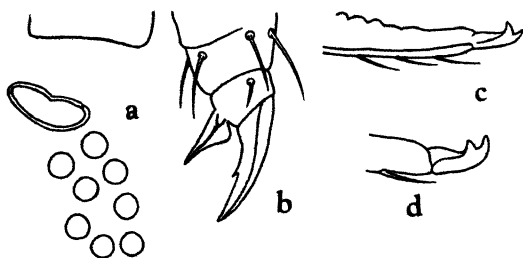


Figure 21—*Proisotoma nigromaculosa* Folsom: a, eyes, postantennal organ and base of antenna of left side; b, right hind foot; c and d, left mucro.

Genus **ISOTOMURUS** Börner, 1903

***Isotomurus palustris balteatus* (Reuter).**

Isotoma balteata Reuter, 1876:86.

Isotomurus palustris variety *balteatus* (Reuter) Schött, 1893:66, pl. 5, fig. 10.

Kauai, Oahu.

Immigrant. Europe, America, Australia, Bismarck Archipelago. First recorded in Hawaii by Folsom (1932:63).

Beneath trash; in soil of sugarcane fields.

Genus **ISOTOMA** Bourlet, 1839

KEY TO THE SPECIES FOUND IN HAWAII

1. Body white; without ocelli, postantennal organs or tenent hairs
..... **minor** Schaeffer.
2. Body purplish yellow; eight ocelli on each side; postantennal
organs present; one tenent hair present. **perkinsi** Carpenter.

***Isotoma minor* Schaeffer (fig. 22, a-e).**

Isotoma minor Schaeffer, 1896:182. Folsom, 1932:63, pl. 6, figs. 67-71, re-description.

Oahu.

Immigrant. Europe, North America, Central America. First recorded from Hawaii by Folsom (1932:63).

In soil of sugarcane fields.

***Isotoma perkinsi* Carpenter.**

Isotoma perkinsi Carpenter, 1904:302, pl. 9, figs. 17-19.

Kauai (type locality: Kaholuamano).

Immigrant(?).

No records are available other than from the unique type.

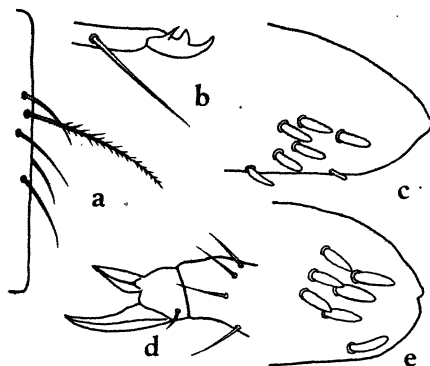


Figure 22—*Isotoma minor* Schaeffer: a, dorsal setae of second abdominal segment; b, left mucro; c and e, apex of left antenna; d, left hind foot.

Family ENTOMOBRYIDAE Börner, 1913

KEY TO THE SUBFAMILIES

1. Dentes slender, dorsally annulated, tapering to small mucrones; mucro short, small..... **Entomobryinae**.
Dentes not annulated dorsally, blunt, with large mucrones..... 2
2. Antennae longer than entire body; ocelli present; dentes without dorsal squamae; mucro robust with dissimilar inner and outer margins; our species yellow with purple maculations. **Paronellinae**.
Antennae shorter than body; ocelli absent; dentes with two dorsal rows of feather-like squamae; mucro elongate, slender, margins similar; our species white..... **Cyphoderinae**.

Subfamily ENTOMOBRYINAE Börner, 1906

Tribe ENTOMOBRYINI Börner, 1906

KEY TO THE GENERA FOUND IN HAWAII

1. Body not squamose 2
Body squamose 3
- 2(1). Tarsal claws each with a large, inner, wing-like, basal tooth; tenent hair of tibio-tarsus weakly developed; with a double row of smooth, pointed bristles on inner face of tibio-tarsus **Sinella** Brook.
Inner basal teeth of tarsal claws simple; tenent hair of tibio-tarsus strongly developed, without such a double row of smooth, pointed bristles on inner face of tibio-tarsus **Entomobrya** Rondani.
- 3(1). Squamae apically pointed, with long, coarse striae; dentes not squamose **Sira** Lubbock.
Squamae apically rounded, with short, fine, close striae; dentes squamose 4
- 4(3). Mucro with two teeth and a basal spine... **Lepidocyrtus** Bourlet.
Mucro falciform **Drepanocyrtus** Handschin.

Genus **SINELLA** Brook, 1882

Sinella caeca (Schött) (fig. 23, a-c).

Entomobrya caeca Schött, 1896:178, pl. 1, figs. 14-16.

Sinella höfti Schaeffer, 1897:192. Folsom, 1932:66, pl. 7, figs. 79-81.

Sinella tenebricosa Folsom, 1902:365, figs. 11-14.

Oahu.

Immigrant. Eurasia, Australia. First recorded from Hawaii by Folsom (1932:66).
In soil, lower forest.

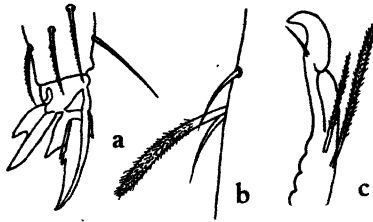


Figure 23—*Sinella caeca* (Schött): a, right hind foot; b, subclavate seta of hind tibiotarsus; c, left mucro and end of dens.

Genus **SIRA** Lubbock, 1869

Sira jacobsoni Börner (fig. 24, a-g).

Sira jacobsoni Börner, 1913:49, fig. 4. Folsom, 1932:66, pl. 8, figs. 82-88.

Sira tricineta Schött, 1917:31, fig. 37.

Oahu.

Immigrant. Java, New Guinea, Sunda Islands, Australia. First recorded from Hawaii by Folsom (1932:66) from specimens collected in 1928.

In soil of pineapple fields; in rice straw.

Genus **ENTOMOBRYA** Rondani, 1861

KEY TO THE SPECIES FOUND IN HAWAII

1. Entirely white species.....**lactea** Folsom.
Yellow with purple markings..... 2
- 2(1). Transversely banded.....**multifasciata imminuta** Folsom.
Not transversely banded..... 3
- 3(2). Yellow with purple lateral stripes; mucro with basal tooth
.....**insularis** Carpenter.
Yellow with confused purple markings; mucro without basal
tooth**kalakaua** Carpenter.

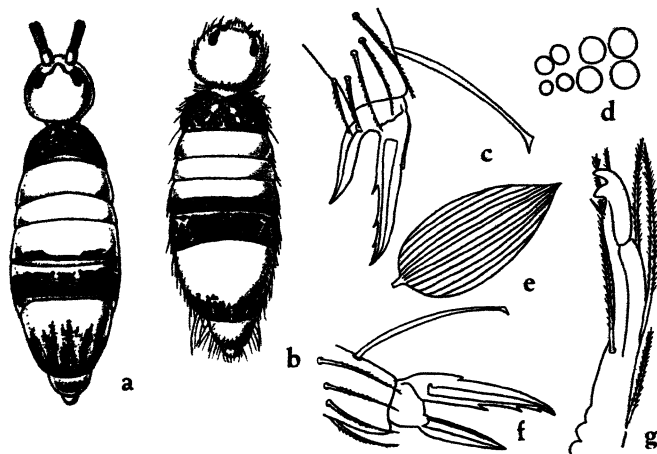


Figure 24—*Sira jacobsoni* Börner: a and b, dorsal aspects to show variation in color pattern; c and f, right middle foot; d, eyes of left side; e, body scale; g, left mucro and end of dens.

***Entomobrya insularis* Carpenter.**

Entomobrya insularis Carpenter, 1904:301, pl. 9, figs. 7–11.

Hawaii (type locality).

Immigrant(?).

***Entomobrya kalakaua* Carpenter.**

Entomobrya kalakaua Carpenter, 1904:301, pl. 9, figs. 12–16.

Kauai (unique type from Kaholuamano).

Immigrant(?).

***Entomobrya lactea* Folsom (fig. 25, a–d).**

Entomobrya lactea Folsom, 1932:65, pl. 7, figs. 76–78.

Oahu (type locality: Honolulu).

Immigrant.

Behind sugarcane leaf sheaths; in trash.

***Entomobrya multifasciata imminuta* Folsom (fig. 26, a–d).**

Entomobrya multifasciata variety *imminuta* Folsom, 1932:64, pl. 7, figs. 72–75.

Oahu (type locality: Pupukea).

Immigrant (the typical variety is almost cosmopolitan).

In soil of pineapple fields. Evidently fungivorous.

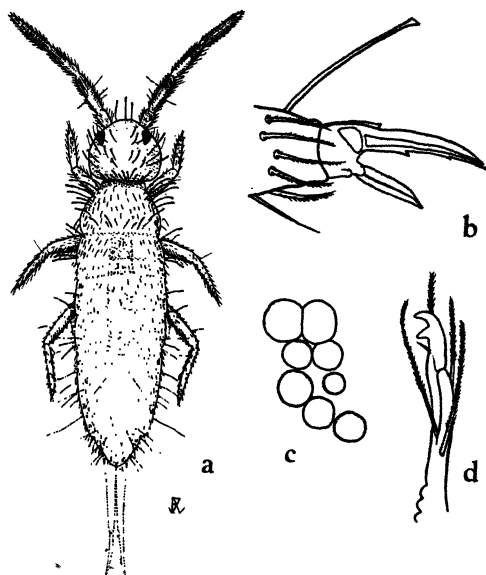


Figure 25—*Entomobrya lactea* Folsom: a, dorsal aspect; b, left hind foot; c, eyes of left side; d, left mucro and end of dens. (a, after Williams, 1931.)

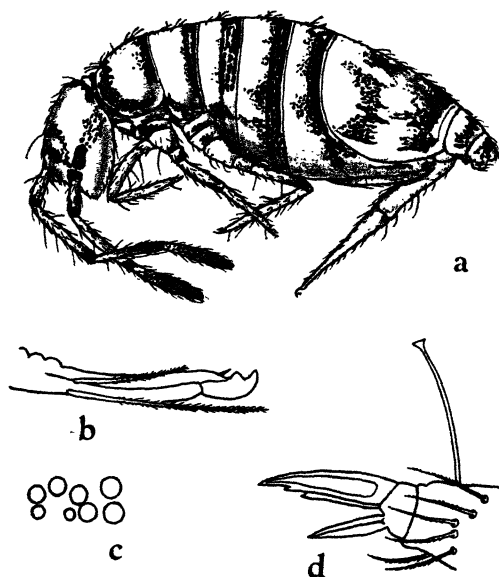


Figure 26—*Entomobrya multifasciata imminuta* Folsom: a, lateral aspect; b, left mucro and end of dens; c, eyes of left side; d, left hind foot.

Genus **LEPIDOCYRTUS** Bourlet, 1839

KEY TO THE SPECIES FOUND IN HAWAII

- Mesonotum extending over base of head; apical tooth of mucro long and slender; white species..... **heterophthalmus** Carpenter.
- Mesonotum not projecting over base of head; apical tooth of mucro short..... 2
- 2(1). Iridescent purple or metallic gray..... **cyaneus** Tullberg.
White or pale yellowish species..... 3
- 3(2). Body entirely white; fourth abdominal segment three to four times as long as third..... **immaculatus** Folsom.
Derm white or pale yellow, most individuals faintly flecked with blue; fourth abdominal segment less than twice as long as third..... **inornatus** Folsom.

Lepidocyrtus cyaneus Tullberg (fig. 27, a-d).

Lepidocyrtus cyaneus Tullberg, 1871:150. Folsom, 1932:68, pl. 8, figs. 89-91.

Oahu.

Immigrant. Cosmopolitan. First recorded from Hawaii by Folsom (1932:68).

In soil of pineapple fields.

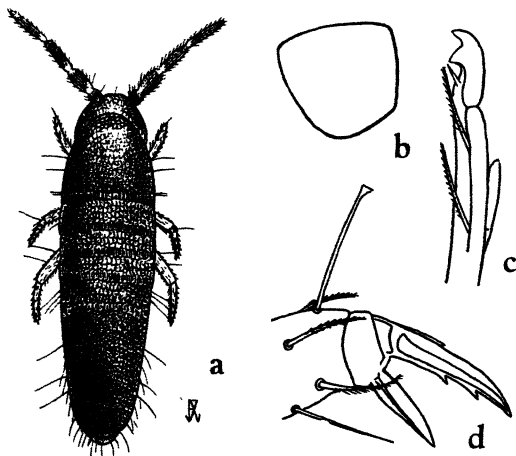


Figure 27—*Lepidocyrtus cyaneus* Tullberg: a, dorsal aspect; b, left aspect of mesonotum; c, left mucro and end of dens; d, right hind foot. (a, after Williams, 1931.)

Lepidocyrtus heterophthalmus Carpenter.

Lepidocyrtus heterophthalmus Carpenter, 1904:300, pl. 9, figs. 1-6.

Hawaii (type series from Kona, 2,000 feet, and Mauna Loa, 4,000 feet).

Immigrant(?).

Lepidocyrtus immaculatus Folsom (fig. 28, c-e).

Lepidocyrtus immaculatus Folsom, 1932:68, pl. 9, figs. 94-96.

Oahu, Maui (type locality).

Immigrant.

In soil of sugarcane and pineapple fields.

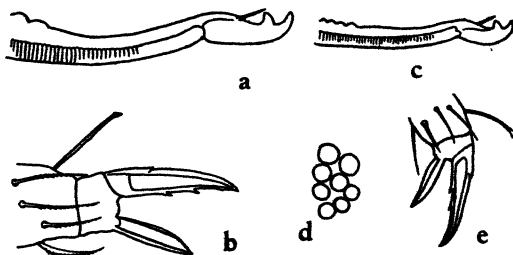


Figure 28—**a-b**, *Lepidocyrtus inornatus* Folsom: **a**, left mucro and end of dens; **b**, left hind foot. **c-e**, *Lepidocyrtus immaculatus* Folsom: **c**, right mucro and end of dens; **d**, eyes of right side; **e**, right hind foot.

Lepidocyrtus inornatus Folsom (fig. 28, a-b).

Lepidocyrtus inornatus Folsom, 1932:68, pl. 9, figs. 92-93.

Oahu (type locality: Honolulu).

Immigrant.

In soil of pineapple fields.

Genus **DREPANOCYRTUS** Handschin, 1925

Drepanocyrtus terrestris Folsom (fig. 29, a-i).

Drepanocyrtus terrestris Folsom, 1932:69, pl. 9, figs. 97-102; pl. 10, figs. 103-104.

Oahu (type locality).

Immigrant.

This is an abundant species, and may be the one reported to build up such large populations in pineapple fields. Common in soil of pineapple and sugarcane fields, under mulching paper, under sugarcane leaf sheaths; it is said to feed on decaying vegetable debris.

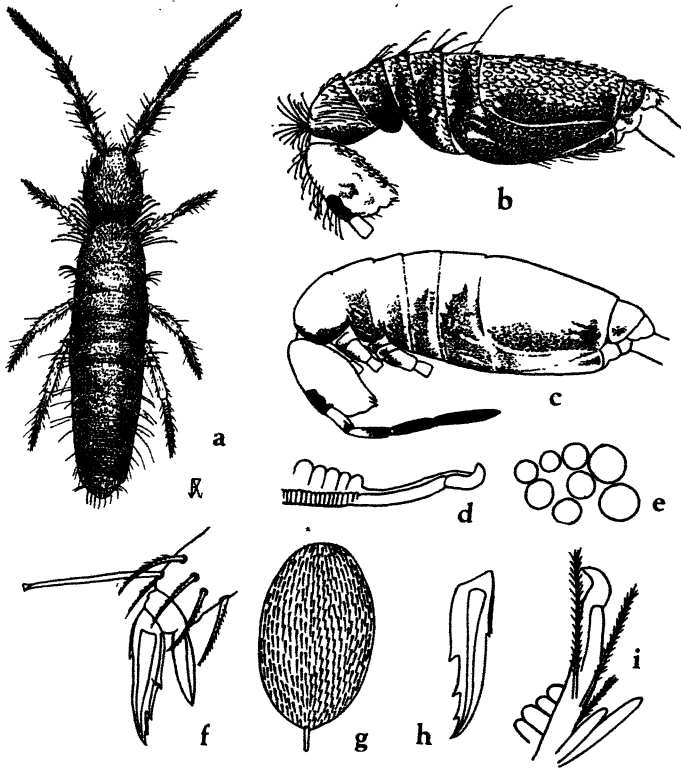


Figure 29—*Drepanocyrtus terrestris* Folsom: a, dorsal aspect (after Williams); b-c, lateral aspects with and without vestiture; d, mucro and end of dens; e, eyes of right side; f, left hind foot; g, a typical body scale; h, unguis; i, left mucro and end of dens.

Subfamily PARONELLINAE
 Tribe PARONELLINI Börner, 1906
 Genus **SALINA** MacGillivray, 1894

Cremastocephalus Schött, 1896:175.

Salina maculata Folsom (fig. 30, a-f).

Salina maculata Folsom, 1932:71, pl. 10, figs. 105-110.

Kauai, Oahu, Hawaii (no more definite type locality given).

Immigrant.

In soil of sugarcane fields; under leaf sheaths of sugarcane; on coffee leaves.

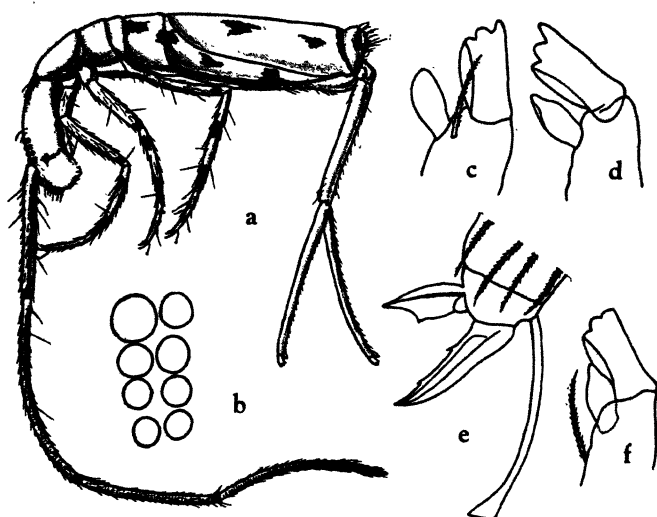


Figure 30—*Salina maculata* Folsom: a, lateral aspect; b, eyes of right side; c, f, right mucro; d, left mucro; e, left middle foot.

Subfamily CYPHODERINAE
 Tribe CYPHODERINI Börner, 1906
 Genus **CYPHODERUS** Nicolet, 1841

Cyphoderus assimilis Börner (fig. 31, a–b).

Cyphoderus assimilis Börner, 1906:181. Folsom, 1932:71, pl. 10, figs. 111–112.

Cyphoderus similis Folsom, 1927:12, pl. 8, figs. 70, 71.

Oahu.

Immigrant. West Indies, Panama (type locality), Java. First recorded from Hawaii by Folsom (1932:71).

Members of this genus are usually myrmecophilous or termitophilous. This species has been found with *Pheidole megacephala* ants in Hawaii.



Figure 31—*Cyphoderus assimilis* Börner: a, left mucro; b, left hind foot.

Suborder SYMPHYPLEONA Börner, 1901

Family SMINTHURIDAE Lubbock, 1870

KEY TO THE SUBFAMILIES

1. Exsertile vesicles of ventral tube with smooth walls; segmentation of thorax evident dorsally.....**Sminthuridinae**.
- Exsertile vesicles of ventral tube with tuberculate walls; segmentation of thorax obsolete..... 2
2. Antennae bent between segments three and four, segment four longer than three; furcula-bearing somite without dorsal papillae**Sminthurinae**.
- Antennae bent between segments two and three; segment three longer than four; furcula-bearing somite with dorsal papillae**Dicyrtominae**.

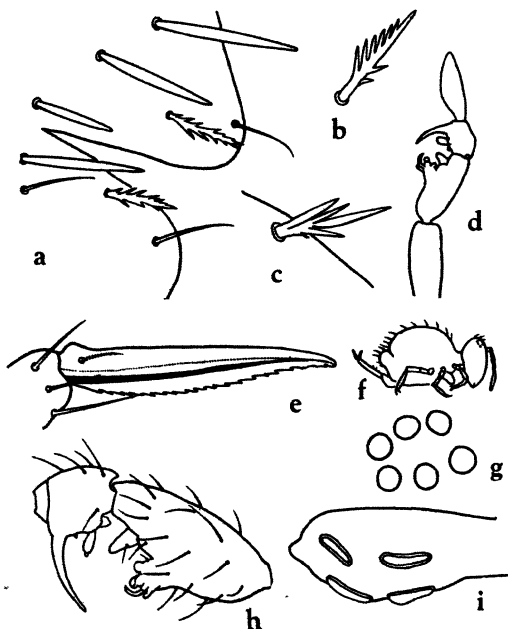


Figure 32—*Sminthurides* (*Denisiella*) *ramosus* (Folsom): a, left aspect of suranal and left subanal lobes of female; b-c, branched setae of left subanal lobe of female; d, left antenna of male; e, left mucro of male; f, lateral aspect; g, eyes of left side; h, second and third antennal segments of male; i, base of fore tibiotarsus of male.

Subfamily SMINTHURIDINAE Börner, 1906

Tribe SMINTHURIDINI Börner, 1913

Genus **SMINTHURIDES** Börner, 1900

Prosminthurus Willem, 1900.

See Folsom and Mills (1938:231-274, 9 pls.) for a revision of the genus with noteworthy discussion.

Subgenus **Denisiella** Folsom and Mills, 1938:264

Sminthurides (**Denisiella**) **ramosus** (Folsom) (figs. 32, a-i; 33, a-f).

Sminthurides ramosus Folsom, 1932:72, pl. 10, fig. 113; pl. 11, figs. 114-123; pl. 12, figs. 124-126.

Sminthurides (*Denisiella*) *ramosus* (Folsom) Folsom and Mills, 1938:266, pl. 8, figs. 94-101, emended description.

Oahu (type locality: Honolulu).

Immigrant. Folsom and Mills (1938:267) say that the closest known relative of this species is *sexpinnatus* Denis of Costa Rica.

In soil of sugarcane fields.

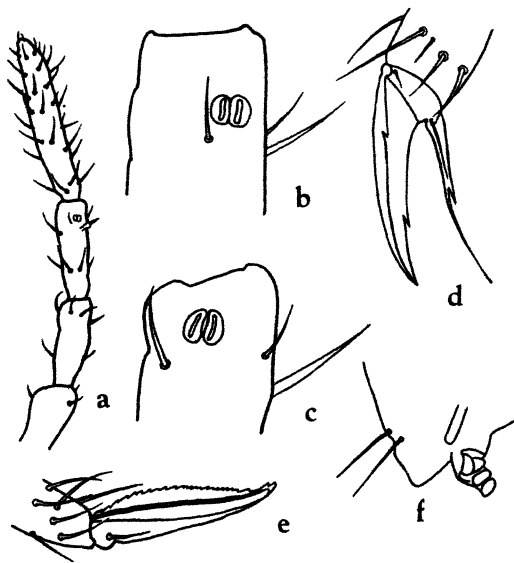


Figure 33—*Sminthurides* (*Denisiella*) *ramosus* (Folsom): a, left antenna of female; b-c, sense organ of third antennal segment of left side of female; d, right fore foot of male; e, left mucro of female; f, left aspect of tenaculum of female.

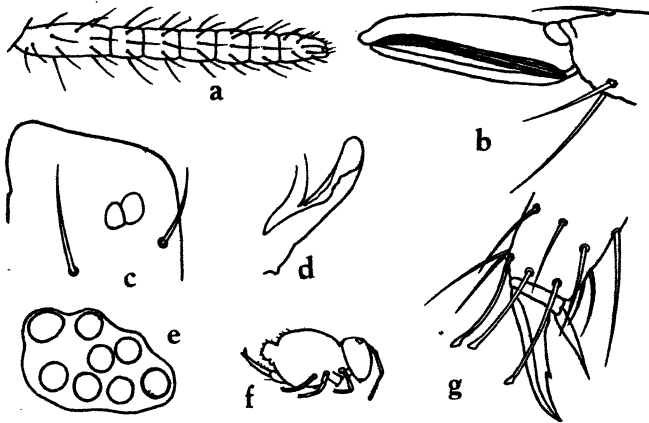


Figure 34—*Bourletiella insula* Folsom: a, fourth antennal segment of female; b, left mucro; c, sense organ of third antennal segment, left side; d, lateral aspect of left subanal appendage of female; e, eyes of left side; f, sketch of lateral aspect; g, left fore foot.

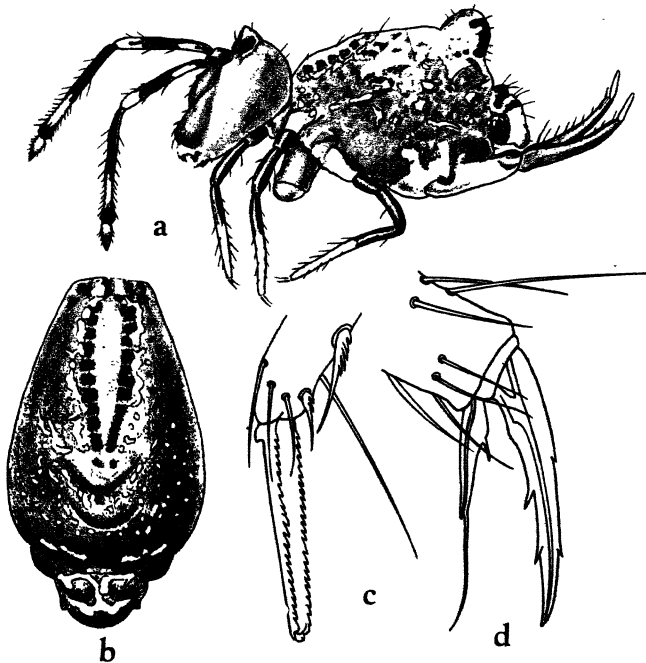


Figure 35—*Ptenothrix dubia* Folsom: a, lateral aspect; b, dorsal aspect of body; c, left mucro; d, left hind foot.

Subfamily SMINTHURINAE Börner, 1906

Tribe BOURLETIELLINI Börner, 1913

Genus **BOURLETIELLA** Banks, 1906

Bourletiella insula Folsom (fig. 34, a-g).

Bourletiella insula Folsom, 1932:73, pl. 12, figs. 127-132.

Oahu (type locality: Honolulu).

Immigrant.

In soil of sugarcane fields.

Subfamily DICYRTOMINAE Börner, 1906

Genus **PTENOTHRIX** Börner, 1906

Ptenothrix dubia Folsom (fig. 35, a-d).

Ptenothrix dubia Folsom, 1932:74, pl. 12, figs. 133-136.

Oahu (type locality: Mount Tantalus).

Immigrant.

On damp rocks along streams.

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A

Subclass PTERYGOTA (Brauer) Lang, 1889

(*pterygotos*, winged)

Pterygonea Brauer, 1885.

The insects of this subclass normally go through a metamorphosis of slight or great degree; they are primarily provided with wings, although most orders have secondarily wingless adults within their ranks; they lack the additional abdominal appendages found in the Apterygota.

Division I. EXOPTERYGOTA Sharp, 1898

(*exo*, outside; *pterygotos*, winged)

Hemimetabola Burmeister, 1829.

Heterometabola Packard, 1888, in part.

This subdivision contains those pterygotan insects which pass through a comparatively simple metamorphosis (wanting in some forms) which is usually without the interpolation of a pupal instar; as a general rule the wings develop externally on the bodies of the nymphs; the young animals are generalized nymphs instead of specialized larvae, and most of them more or less resemble the adults, with the exception that the wings and sexual organs are not developed.

Order ORTHOPTERA Olivier, 1789

(*orthos*, straight; *pteron*, wing)

Cockroaches, Grasshoppers, Locusts, Mantids, Katydid, Leaf Insects,
Stick Insects, Crickets

Of the seven families of Orthoptera accepted by more conservative workers, five have representatives in Hawaii. The two families not found in our fauna are the Phasmidae (stick and leaf insects, widespread and common in the tropics especially) and the Grylloblattidae (a group of a few peculiar, cricket-like insects found under stones in certain restricted snowy mountain regions of western North America and in Japan). Of the five families found in Hawaii, only the Tettigoniidae and Gryllidae are represented in the native fauna. All of the members of the other three families are extrinsic.

Compound eyes and ocelli present in most species; antennae moniliform or filiform, greatly elongated in some families; mouth parts generalized, exposed,

masticatory, mandibles strongly developed, with two articulations with the head; wings variable, secondarily absent, incompletely developed, fore wings only present or all strongly developed; venation generalized, complex, supernumerary veins and primitive vein network (*archedictyon*) common; fore wings (*tegmina*) usually narrower than hind pair, thickened, leathery and modified to give protection to hind pair; hind wings membranous, folded fan-like longitudinally, also folded transversely in some forms when at rest, vannal area strongly developed; abdomen usually with 10 evident segments, the remainder modified or wanting, cerci present in our species, segmented or not; ovipositor reduced and concealed in Blattidae and Mantidae, exerted and distinct in Acrididae, Tettigoniidae and Gryllidae (except *Gryllotalpa*); legs saltatorial, cursorial, raptorial or fossorial; tarsal segments variable, from none to five; stridulation characteristic among Saltatoria, and tympanal organs present in the stridulating groups; ovoviviparous or oviparous, some species parthenogenetic; eggs laid singly or in groups, inserted in plant tissue or in soil, enclosed within a characteristic capsule (*ootheca*) in Blattidae and Mantidae; some species fitted with repugnatorial glands; phytophagous, predaceous or omnivorous.

This order has the most ancient lineage of contemporary insects, and its fossil record is considered the most completely known. Cockroaches, for example, were much more common far back in the Upper Carboniferous, when they apparently reached their zenith of development and diversity, than they are today. It does not follow, however, that all orthopterans are ancient insects, for some groups (our modern Acridinae, for example) are not represented as fossils until Pleistocene times.

Orthoptera are pre-eminently a tropical group, although many species are found in temperate zones. The greatest diversity of forms is found in the tropics of the Eastern Hemisphere. More than 20,000 species have been described.

This order contains no minute insects, and, comparatively speaking, the average orthopteran is a rather large insect. Perhaps the most bulky of living insects belong here, and certainly some of the Phasmidae are the longest of contemporary insects, for some exceed 10 inches in length. Some of the most bizarre and remarkable organisms of the Animal Kingdom are found in the order.

Orthoptera have attracted many students, and a great body of data is amassed about many phases of the group, from fossil history and embryology to musical ability and psychology. The group has retained some generalized or primitive types of structure and has been much used in laboratories for purposes of instruction and experimentation. Contrary to popular belief, however, the animals are not entirely "primitive" in structure because many parts of their bodies are highly evolved or specialized.

The economic importance of the order hardly needs emphasis. The great plagues of locusts, the devastation wrought and influence on man are commonplace in ancient and modern history of many lands. Even today with all our highly developed methods for combating such hordes, millions of dollars worth of damage is done every year on all of the continents because of the ravages of Orthoptera

upon man's crops. Corps of technicians are employed constantly in studying the detrimental species, and each year thousands of square miles of land are strewn with poisons in attempts to control the pests. Fortunately for us in Hawaii, comparatively little damage is done by Orthoptera, but several of the species found here are pests; some cause material damage, and the mere presence of others constitutes a general nuisance. The importation of additional, more harmful species is an ever-present possibility.

Many kinds of parasites are known to attack various Orthoptera, and they are discussed under each family. Parasites other than those already attacking various species in Hawaii are known elsewhere, and these should be investigated with the purpose of introduction in mind.

The bulk of our species are nocturnal, and the layman seldom comes in contact with more than a few of our more than 80 species. Members of the group are to be found throughout Hawaii from seashore to mountain top. Without exception, the lowland species are immigrants, but our forests have a most interesting fauna of native species, some of which belong to unusual endemic genera.

I have not given detailed or complete synonymy here, but such data are available in the literature cited in the bibliography, especially in the works of Kirby (1904, 1906, 1910) and Hebard (1922, 1933).

TABULAR ANALYSIS OF THE HAWAIIAN ORTHOPTERA

FAMILY	GENERA	ENDEMIC GENERA	NON- ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Blattidae	15	0	15	18	0	18
Mantidae	3	0	3	3	0	3
Acrididae	3	0	3	3	0	3
Tettigoniidae	6	2	4	16	12	4
Gryllidae	11	3	8	42	33	9
Totals	38	5	33	82	45	37

Percentage of endemism in native group: genera, 100 percent; species, 100 percent.

Percentage of present-day fauna native: 54 percent.

Percentage of present-day fauna adventive: 45 percent.

Average number of species per genus in native group: 9.

Average number of species per genus in adventive group: 1.2.

KEY TO THE FAMILIES OF ORTHOPTERA FOUND IN HAWAII

1. Tarsi five-segmented; hind legs not much larger than others, not developed for leaping; head deflexed and more or less concealed beneath pronotum or entirely exposed and then with fore legs raptorial. 2
- Tarsi with four segments or less; hind legs either strongly developed for leaping and larger than others or not developed for leaping and with three-segmented tarsi and with fore tibiae and tarsi remarkably modified for burrowing (*Gryllotalpa*), and otherwise not as above; Suborder Saltatoria 3

- 2(1). Head deflexed and concealed beneath shield-like pronotum;
 Suborder Cursoria (cockroaches) **Blattidae**.
 Head not at all concealed, broader than the elongate, neck-
 like prothorax, fore legs raptorial (fitted with strong spines
 and modified for grasping prey); Suborder Gressoria
 (mantids) **Mantidae**.
- 3(1). Antennae not longer than one-half the body (but fore legs
 never fossorial); ovipositor short and comparatively incon-
 spicuous, never blade-like; tarsi three-segmented; tympana
 located on sides of first abdominal segment.....
 (short-horned grasshoppers) **Acrididae**.
 Antennae usually as long as, or much longer than, body (less
 than one-half as long as body in *Gryllotalpa* only); tarsi
 three- or four-segmented; ovipositor usually, not always,
 long and blade-like, sickle-shaped or cylindrical (concealed
 only in *Gryllotalpa* and slender and sometimes compara-
 tively obscure in *Myrmecophila*); tympana situated on fore
 tibiae (wanting in *Myrmecophila*)..... 4
- 4(3). Tarsi four-segmented
 (longhorned grasshoppers, katydids) **Tettigoniidae**.
 Tarsi three-segmented..... (crickets) **Gryllidae**.

Suborder CURSORIA (Latreille, 1817)

Family BLATTIDAE (Burmeister, 1840)

Blattariae Latreille, 1810.

Blattaria Burmeister, 1829.

Cursoria Westwood, 1839.

Blattoidea Brunner, 1882.

Oothecaria Escherich, 1914.

Cockroaches, Roaches; Hawaiian name: "elehu"

Swift-running animals of depressed form, usually ovate; head concealed or almost concealed beneath pronotum, directed ventro-caudad so that the face is almost horizontal when at rest; antennae inserted below eyes, long and filiform, segments short, multitudinous; compound eyes usually large, reniform; ocelli or ocellar spots (*fenestrae*) present; mandibles large, dentate; maxillary palpi five-segmented; labial palpi three-segmented; pronotum large, shield-like; tegmina and hind wings variable, present or absent, subject to sexual dimorphism, abbreviated or longer than abdomen, tegmina held flat over pterothorax and abdomen and overlapping when at rest; abdomen 10-segmented, usually only seven or eight tergites visible, females with seven visible ventrites, males with nine; tenth tergite called the *supra-anal plate* and bearing the segmented cerci; seventh or ninth ventrite called the *subgenital plate* and bearing a pair of unsegmented *styles* in the males; ovipositor wanting; legs with coxae large, broad, depressed, plate-like, femora compressed, tibiae strongly spinose, tarsi five-segmented, fifth segment

with or without arolia between the widely separated, paired elaws, first four segments usually with pulvillae; oviparous or ovoviviparous, some forms producing characteristic *oothecae* (egg cases).

The cockroaches hardly need a detailed introduction, for they and their nocturnal activities are well known to the average resident of Hawaii. There are 18 species included in 15 genera found here; all of them are immigrants. The number of cockroaches described from the world is probably near 1,500 species, and they are predominantly insects of the tropics. However, temperate zones are not entirely without endemic representatives of the family, and several cosmopolitan species are regular residents of temperate countries.

Dr. J. A. G. Rehn has said (1945:265):

The cockroaches are insects which to the average person are house-haunting pests, living secretive lives away from the light of day, and creeping into one's larder when given the slightest opportunity. Most definitely they produce in the majority of people a strong feeling of aversion. It often takes some effort to convince the "doubting Thomases" that the number of species of cockroaches which are domiciliary pests is greatly limited—in fact less than one percent of the known forms—and that cockroaches of many kinds are diurnal, with hundreds of species tropical forest foliage forms, others semiaquatic, some in one sex living in the ground, a few wood-boring, while a dozen or so genera will be found, in a state of either known or suspected commensalism, in the nests of ants, wasps, or termites.

This paper by Dr. Rehn should be consulted also for an interesting account of the original homes and the dispersal of the "domestic" roaches.

Fossil cockroaches are abundant in many horizons; in fact, over 90 percent of the insects of some Upper Carboniferous deposits are said to be cockroaches. However, their dominant position has been lost with the ages, for they now compose only a fraction of 1 percent of present-day insects. Their fossil record is the most complete of the Insecta, and they are, as a group, considered among the oldest of winged insects.

Cockroaches have well-developed powers of organ regeneration, and may regenerate legs, antennae and cerci if these organs are broken. Some species are known to have prelocalized points of weakness in their legs and antennae, at which places it is usual for the appendages to break if damaged. A worthwhile paper on regeneration is that by Woodruff (1937), which includes a good bibliography.

One of the most interesting features of the Blattidae is the peculiar egg cases produced by most species. These *oothecae* are formed by the female over a period of several days as her eggs mature. They consist of a purse-like or seed-like structure composed of a hardened material secreted by accessory genital glands. Each is divided lengthwise into two compartments in which the eggs are set upon end, a longitudinal row in each compartment. When the batch of eggs has been completely enclosed, the female roach attaches it in some protected place, or it is dropped loosely. Female roaches often are seen with partially formed *oothecae* protruding from their abdomens. The size, shape, design and number of eggs included vary with the species, and many of the *oothecae* are diagnostic and enable one to name easily the species of roach depositing the egg case. The young hatch-

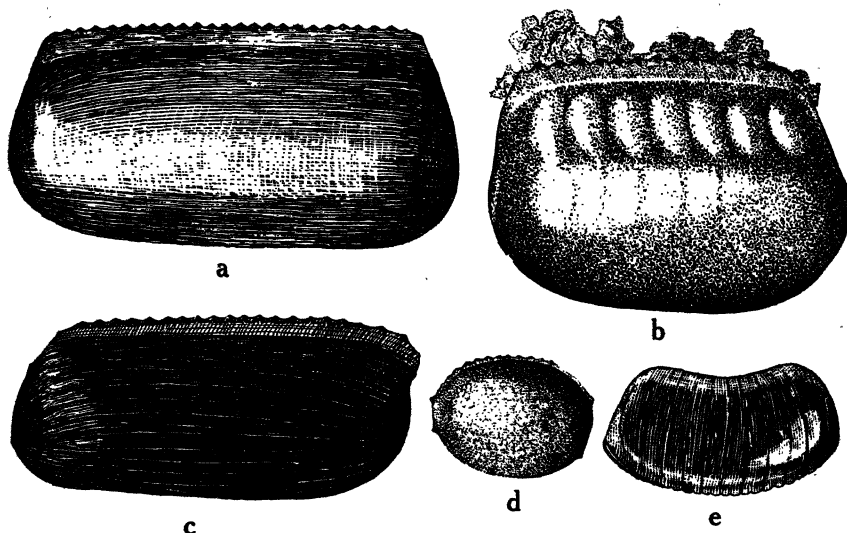


Figure 36—Some cockroach egg cases (oothecae): a, *Periplaneta australasiae* (Fabricius); b, *Periplaneta americana* (Linnaeus); c, *Cutilia soror* (Brunner); d, *Euthyrrhapha pacifica* (Coquebert); e, *Symploce hospes* (Perkins). (Drawings by Williams, 1931.)

ing from the oothecae produce the characteristic batches of individuals of similar size that we see so often in our homes.

Most cockroaches are omnivorous feeders, and the so-called "domestic" species feed upon almost any edible thing they can find—even their fellows when opportunity permits—including all sorts of food stuffs, book bindings, paper, wall paper, starched clothing, woolens, glued and pasted articles, labels, living and dead insects (often seriously damaging unprotected museum specimens), dead organic matter, leather, sweets, starchy or farinaceous materials; some feed upon the roots, bark, foliage, flowers, and fruits of various plants out-of-door^s. Some "domestic" species eat flowers of various plants when they are established in unsettled places such as uninhabited islands. I have even had them gnaw on my feet while sleeping on a copra schooner traveling in Fijian waters. The damage they do to paper and book bindings is easily confused with that of silverfish. Their feces soil every place they frequent, and their presence in closets and kitchen cupboards is thus easily ascertained even though the cockroaches may be hidden away in cracks and crannies. Some species throw off a disagreeable musk and at times may thus spoil food and give a most unwholesome and persistent odor to anything with which they come in contact; drawers and cupboards frequented by them become fouled and obnoxiously odoriferous.

Cockroaches have many enemies, both parasitic and predaceous. In Hawaii there are two species of *Evania* wasps which parasitize the oothecae of several kinds of cockroaches, as do the small wasps, *Solindenia picticornis* Cameron and *Comperia*

*falsicornis** (Gomes). Dr. Williams recently introduced the brilliantly colored "jewel wasp," *Ampulex compressa* (Fabricius), from New Caledonia as an additional parasite for our larger cockroaches (for a detailed and most readable, well-illustrated account of this species see Williams, 1942:221). *Dolichurus stantoni* Ashmead, a small Philippine wasp, is also an introduced parasite. The eulophid hypoparasite *Tetrastichus hagenowii* Ratzeburg attacks the *Evania* parasites in the oothecae and may be erroneously thought to be a parasite of the cockroach eggs when observed emerging from them. The introduced toad, *Bufo marinus*, eats quantities of cockroaches as do geckoes, skinks and mongooses, and sparrows and mynah birds catch a share. Chickens and other barnyard fowl eat quantities of these insects when they can get them, but, unfortunately, one of the roaches most likely to be eaten is an intermediate host for Manson's eye worm. Our larger spiders are effective cockroach hunters, and the large, harmless but tarantula-like *Heteropoda regia* (Fabricius) frequently found in buildings is especially adept in catching roaches and should be harbored rather than killed, as often is done in many households.

Few insects have had more methods suggested for their control, some of them good, many ineffective. As with silverfish, one of the most effective methods of clearing a building of the pests is cyanide fumigation, but it is not always possible to use this deadly gas, and other methods of control must be resorted to. It should be borne in mind, however, that although a room or a building may be cleared of roaches by fumigation, it may become rapidly reinfested by the influx of specimens from the outside. A standard DDT 5 percent spray or 10 percent dust is coming into common use and is a simple and very effective method of control. DDT is replacing rapidly the older methods of control which are listed hereafter. It should be sprayed or dusted in places where the cockroaches will run over it. Powdered pyrethrum or sodium fluoride, or a combination dust including both poisons, dusted about places frequented by the pests is an easy and efficient method to aid in their control, and was, perhaps, the method most usually recommended before DDT came into use recently. In place of pyrethrum or sodium fluoride, powdered borax, which is a common ingredient in commercial roach powders, may be used. It may also be mixed with ground chocolate at the rate of one part borax to three parts chocolate and used as a poisoned bait. Some people in Hawaii report excellent control by the use of a bait consisting of one tablespoon of sugar mixed with one cup of borax. A trap similar to that used for silverfish, but baited with molasses, rancid butter, wine, beer or other alcoholic beverage, or most any readily eaten food as bait may be used. Such traps may be used safely near food or where children or pets have access to them. An unusual method of control recommended by some workers is to mix one part of plaster of Paris with three or four parts of flour. This mixture is placed in a plate, and close by is placed a shallow plate of water containing paper or similar article to enable the roaches to drink readily. The roaches will eat the plaster and flour mixture, become thirsty, drink the water which sets the plaster and thus clog the digestive tract causing death. A poison paste made from 1 or 2 percent phosphorus in sweetened flour is said to be effective.

tive and, certainly, if eaten would be a deadly poison. Arsenical baits* are not effective. A number of baits, dusts and sprays are available from many commercial dealers. A spray of some such material as "Flit" is temporarily effective for use in cabinets, closets and cupboards. Naphthalene (flakes or moth balls) and paradichlorobenzene crystals are effective in keeping cockroaches out of closed containers, drawers, closets, etc., and will kill the insects if in sufficient concentration. Stored materials (other than foodstuffs) susceptible to attack should always be protected with an ample supply of some such fumigant and then sealed. To protect book bindings and similar articles, the liquid poison outlined in a previous chapter for the control of silverfish is recommended.

No matter how clean and careful the inhabitants, cockroaches will gain entrance to most homes in Hawaii. The pests are masters at the art of entering buildings in the most devious of ways. To combat the roaches successfully, kitchens, pantries and dining areas should be kept spotlessly clean, no food should be exposed overnight, all cracks around windows and outside doors (especially at the floor edges of the doors, which are common points of entry) that are large enough for roaches to enter should be made tighter and proper garbage disposal is essential for effective control. Of course, all oothecae found should be immediately destroyed, and they should be searched for in closets, above and behind drawers, on the undersides of chairs and tables, and in similar obscure places. Even with these precautions and the use of poisons and traps, cockroaches will gain entrance, but their numbers will be small. If one darkens the kitchen for an hour or so at night, then enters and turns on the light, he may kill many roaches with a fly swatter. This method, although elementary, is quite effective in keeping the populations at a minimum and is to be recommended. I have found a solution of DDT (which has come into use since this text was written) painted on the lower edges of outside doors and thresholds, along base boards, and along the inside corners of cupboards an excellent agent in control.

Decoctions of cockroaches are used medicinally in various places, and even yet are listed in some pharmacopoeia.

The name cockroach is said to be a corruption of the Spanish "cucuracha."

Because cockroaches are such common insects, I feel that a simplified key to the 18 species now known to occur in the islands will be more useful than one based upon characters used to differentiate the subfamilies, some of which are not easily seen nor understood by workers unfamiliar with the group.

SIMPLIFIED KEY TO THE COCKROACHES FOUND IN HAWAII

(Adults)

1. Tegmina developed, either brachypterous or fully formed,
but always concealing pterothorax at least..... 2
- Tegmina reduced to small pads which do not completely
conceal the meso- or metathorax, excepting *Loboptera*
dimidiatipes, on which the mesonotum is concealed and
the metanotum is exposed only at middle behind.....15

- 2(1). Small to medium-sized species, less than 20 or 22 mm. in length 3
Large to very large species, over 22 mm. long, usually longer than 25 mm. 11
- 3(2). Thorax and tegmina rather dull, densely punctate or roughened, conspicuously hairy; tegmina leathery, densely opaque, veins not well-marked. 4
Thorax and tegmina shiny, not hirsute; tegmina translucent or partly transparent, veins conspicuous. 6
- 4(3). Broad species, up to more than 15 mm. in length; hairs on dorsum short. **Diploptera dytiscoides** (Serville).
Small species, less than 10 mm. long; hairs on dorsum long; anterior and lateral pronotal margins with many long erect setae 5
- 5(4). Each postero-lateral corner of pronotum with a conspicuous, well-defined, yellow spot; a conspicuous, sharply marked, round, yellow spot just behind middle of tegmina; pronotum and tegmina otherwise black.
..... **Euthyrrhapha pacifica** (Coquebert).
Without such well-defined spots; pronotum and tegmina brown; a tiny species about 5 mm. long.
..... **Holocompsa fulva** (Burmeister).
- 6(3). Pronotum either almost entirely dark-colored (nearly or quite black), or with two dark vittae, as in figures 40, 49... 7
Pronotum not so colored. 8
- 7(6). Nearly 20 mm. long; pronotum entirely dark excepting for pale lateral and anterior margins; tegmina with a dark vitta at shoulder. **Pycnoscelus surinamensis** (Linnaeus).
Usually less than 15 mm. long; pronotum with a pair of characteristic dark vittae, otherwise pale. 7a
- 7a(7). Male terminalia as in figure 39. **Blattella germanica** (Linnaeus).
Male terminalia as in figure 39. **Blattella lituricollis** (Walker).
- 8(6). Hind margin of pronotum strongly convex, its middle part obviously produced backward so that each side of hind margin extends obliquely forward from middle to sides
..... **Symploce hospes** (Perkins).
Hind margin of pronotum subtruncate or feebly convex. 9
- 9(8). Tegmina with large numbers of conspicuous cross-veins, veins and cross-veins outstanding and forming a characteristic net-like pattern because of their nearly white coloring; disk of pronotum with narrow, irregular, vermiform, brown markings. **Graptoblatta notulata** (Stål).
Not as above; cross-veins mostly inconspicuous. 10
- 10(9). Species found in dwellings and buildings; with both brachypterous and long-winged forms; wings in long-winged form reaching far behind apex of abdomen to beyond apices of cerci which are thus well-concealed; penultimate segment of maxillary palpi longer than distance between eyes; pronotum not strongly transverse, more strongly narrowed anteriorly, as in figure 42.
..... **Supella supellectilium** (Serville).

- Forest species; no brachypterous forms; wings reaching only slightly behind apex of abdomen and leaving cerci exposed and projecting conspicuously caudad of wing apices; penultimate segment of maxillary palpi obviously shorter than interocular distance; pronotum strongly transverse, nearly twice as broad as long.
 **Allacta similis** (Saussure).
- 11(2). Mahogany or reddish-brown species. 12
 Yellowish or grayish-brown species. 14
- 12(11). Tegmina with a rather broad, long, yellow, costal vitta at base; pronotum with a complete yellow ring sharply contrasting in color with the dark central part and equally dark margin. **Periplaneta australasiae** (Fabricius).
 Humerus of tegmina without a pale vitta and pronotum not so colored, the color pattern less definite. 13
- 13(12). Supra-anal plate with a deep, narrow, acute, median emargination. **Periplaneta americana** (Linnaeus).
 Supra-anal plate convex in male, broadly emarginate in female. **Periplaneta brunnea** Burmeister.
- 14(11). A very large species, usually distinctly more than 40 mm. long; wings extending beyond apex of abdomen, usually far beyond. **Leucophaea maderae** (Fabricius).
 Less than 30 mm. long; wings not or hardly reaching apex of abdomen, or at most barely surpassing apex.
 **Nauphoeta cinerea** Olivier.
- 15(1). Large, robust species, 25 or more mm. long; thoracic nota all irregularly marked with yellow over disks; supra-anal plate with a strong, median, V-shaped notch.
 **Neostylopyga rhombifolia** (Stoll).
 Smaller species less than 20 mm. long; thoracic nota with yellow margins only, not marked on disk. 16
- 16(15). Tegmina reduced to small scales at sides of mesonotum; length between 15 and 20 mm. **Cutilia soror** (Brunner).
 Tegmina concealing mesonotum and most of metanotum; a small species usually less than 10 mm. long.
 **Loboptera dimidiatipes** (Bolivar).

Subfamily ECTOBIINAE

Genus **ALLACTA** Saussure and Zehntner, 1893**Allacta similis** (Saussure) (fig. 37).*Blatta similis* Saussure, 1870:245.*Phyllodromia obtusata* Brunner, 1895:892; described as a Hawaiian species.*Allacta similis* (Saussure) Hebard, 1922:327.

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii.

Immigrant. Australia. First recorded in Hawaii by Brunner (1895:892). Considered endemic until 1922.



Figure 37—*Allacta similis* (Saussure).

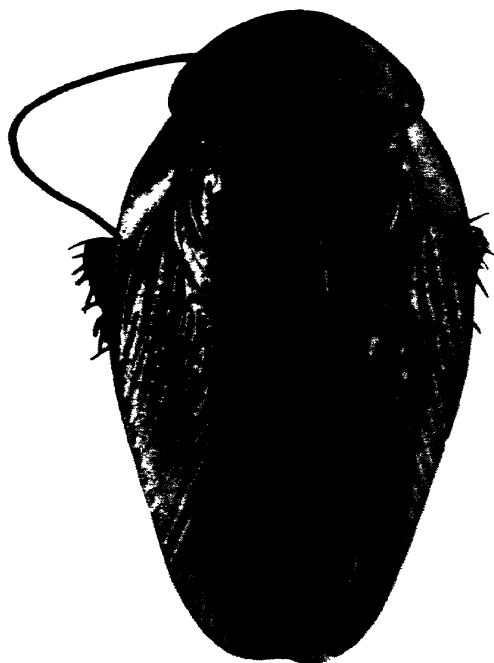


Figure 38—*Graptoblatta notulata* (Stål).

Common under bark, among leaves and clusters of foliage, in hollow stems and on many kinds of plants in forests. Variable and polymorphic.

Parasites: *Solindenia picicornis* Cameron (Hymenoptera: Encyrtidae) in oothecae; *Dolichurus stantoni* Ashmead (Hymenoptera: Ampulicidae) on nymphs.

Predators: some endemic birds (Perkins, 1913:ccxiv).

Genus **GRAPTOBLATTA** Hebard, 1929

Eoblatta Shelford, 1911, not Handlirsch, 1906.

For notes on generic names, see Rehn, 1931:297-304.

Graptoblatta notulata (Stål) (fig. 38).

Blatta notulata Stål, 1860:308; type locality: Tahiti.

Phyllodromia hieroglyphica Brunner, 1865:105.

Eoblatta notulata (Stål), Hebard, 1922:329, pl. 26, fig. 11. Chopard, 1929:17, fig. 12.

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii, Kure (Ocean).

Immigrant. Widespread in Oceania, Malay Peninsula, Sumatra, Java, Borneo, Celebes, New Guinea, New Caledonia, New Hebrides, Fiji, Samoa, Tahiti, Marquesas, Tuamotus, Easter Island. First recorded from Hawaii by Bormans in 1882.

Subfamily PSEUDOMOPINAE

Genus **BLATTELLA** Caudell, 1903

KEY TO THE SPECIES FOUND IN HAWAII

1. Male terminalia as in figure 39; left phallomere slender distad, rather sickle-shaped and not inflated on inner side of distal curvature; virga with edge obliquely grooved distad; supranal plate not over one-half length of cercus, usually shorter **germanica** (Linnaeus).
2. Male terminalia as in figure 39; left phallomere expanded on inner side of apical curvature and the resulting arcuation dentate, the apical filament-like process conspicuously twisted (like a screw); virga without conspicuous grooves; supranal plate about two-thirds as long as a cercus. **litoricollis** (Walker).

Blattella germanica (Linnaeus) (fig. 39).

Blatta germanica Linnaeus, 1767:668; type from Denmark.

The German cockroach; croton bug.

Kauai, Oahu, Molokai, Maui, Hawaii, Laysan.

Immigrant. First recorded from the Territory by Perkins (1899:5). Cosmopolitan; an "international" pest; originally a North African species.

This does not seem to be a common species in Hawaii under present, normal

conditions. However, it has been reported occasionally in the past as "swarming" in shops and houses in the islands. During the recent war it became a pest in barracks and kitchens in some newly erected military establishments. It is abundant on many ships docking here. It is not a common cockroach in island homes—*Supella* has that distinction. The field roach, *Blattella lituricollis* (Walker) (which see), rarely enters homes, but it is easily confused with and has been wrongly called *germanica* in our records.

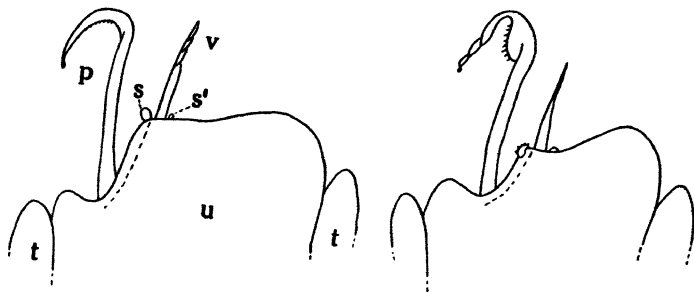


Figure 39—Terminalia of male *Blattella* as seen from beneath with parts extruded: left, *B. germanica* (Linnaeus); right, *B. lituricollis* (Walker). p, left phallomere; t, edges of ninth tergite; u, subgenital plate (ninth sternite); s, s', left and right styles; v, virga. The phallomere and virga are usually concealed and may have to be dissected out to be seen. (After sketches kindly supplied for this work by A. B. Gurney.)

***Blattella lituricollis* (Walker) (figs. 39, 40).**

Blatta lituricollis Walker, 1868:105.

The false German cockroach.

Oahu, Molokai, Hawaii, and probably all the islands, but material at hand inadequate to determine exact range.

Immigrant. An Oriental species known from China, Burma, Philippines, East Indies; (type locality: Amoy). Although present in the islands for many years, it has been confused with *Blattella germanica*.

This is a common, widespread roach of fields in Hawaii. I have found it especially abundant among grasses and weeds along roadways and curbs. It rarely enters dwellings, and, from my experience, it appears that when it is found in a dwelling it is there because it has lost its way, not because of choice. It is frequently attracted to lights. It is very rapid in its movements and is difficult to capture.

The pale oothecae are carried by the female until the young are ready to hatch. I have had the nymphs emerge a few minutes after capturing a female carrying an egg case.

This species is so closely similar to *Blattella germanica* that it was confused with that species in Hawaiian collections until 1946. Dr. Ashley B. Gurney, of the United States National Museum, kindly examined a series of specimens and made

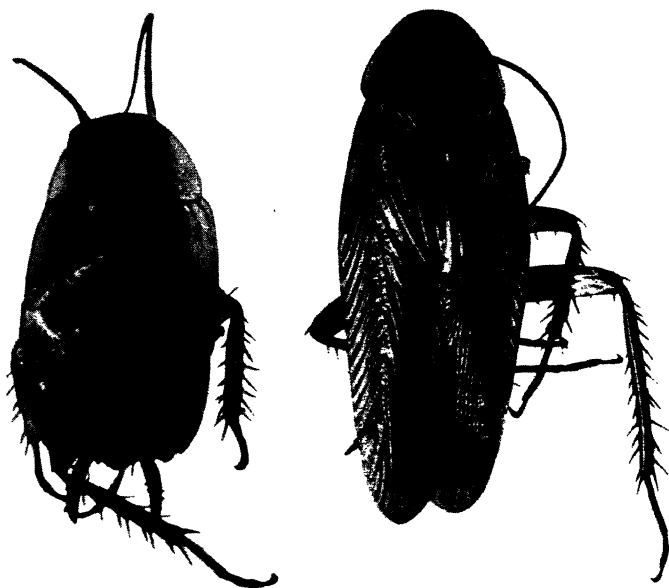


Figure 40—*Blattella lituricollis* (Walker), the false German cockroach, nymph and adult.

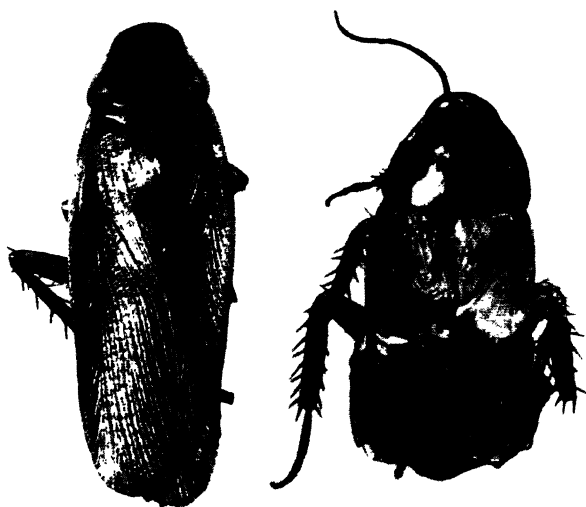


Figure 41—*Symploce hospes* (Perkins). Male, left; female, right.

the identification of this species following his reading of my manuscript notes on the habits of this form in the islands. It is somewhat smaller (10–12 mm. long) and more delicate than *B. germanica*, and the male terminalia are quite distinctive, as the illustrations indicate.

Genus **SYMPLOCE** Hebard, 1916:355

Symploce hospes (Perkins) (figs. 36, e; 41).

Phyllodromia hospes Perkins, 1899:5; type series from Kauai and Oahu (Honolulu).

Symploce lita Hebard, 1916:357, pl. 17, fig. 8; pl. 18, figs. 1–4.

Symploce hospes (Perkins) Hebard, 1922:330. Williams, 1931, pl. 2, fig. 4. ootheca.

Kauai, Oahu, and probably the other islands.

Immigrant. Southern United States; Central America. First recorded from Hawaii by Perkins (1899:3).

Common under stones, in rubbish, abundant in grass and weeds.

Female brachypterous; 30 to 40 oothecae produced per year at 3- to 10-day intervals; incubation period about 6 weeks. Bionomical studies by Illingworth (1915: 138).

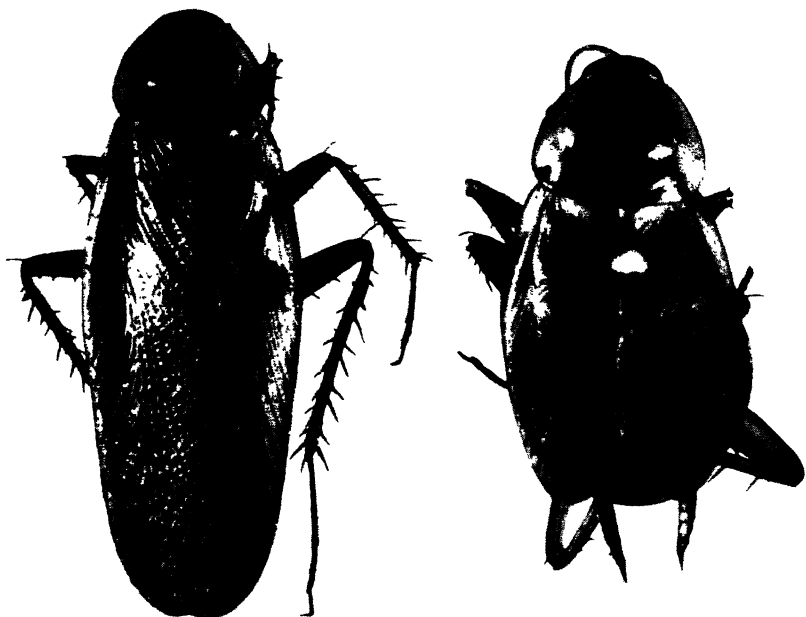


Figure 42—*Supella supellectilium* (Serville), the brown-banded cockroach. Male, left; female, right.

Genus **SUPELLA** Shelford, 1911**Supella supellectilium** (Serville) (fig. 42).*Blatta supellectilium* Serville, 1839:114.

The brown-banded cockroach.

Oahu, Molokai, Maui.

Immigrant. Tropicopolitan; originally an African species. Australia, Fiji, California, Florida, Central and South America. First recorded from Hawaii by Swezey in 1921 from specimens collected at Honolulu.

Parasite: *Comperia falsicornis* (Gomes) (Hymenoptera: Encyrtidae), on the eggs.

This species resembles closely our *Symploce*, but it can be separated easily by the different shape of the pronotum, which in this species is subtruncate behind instead of being produced caudad in the middle as in *Symploce hospes*. The females are brachypterous.

Until recently, this was the commonest cockroach in residences in Honolulu. However, since the accidental importation of the splendid *Comperia* egg parasite, the species has been practically wiped out in some places. For a number of years my own home supported continuously a healthy population of *Symploce*, but since I began work on the parasites, I have had difficulty in finding oothecae for experimental purposes. I have spread the parasite to other parts of Honolulu and have had success in controlling the roach in a store building. As many as 20 parasites were reared from one ootheca, and in some surveys I have found nearly 100 percent parasitism of all oothecae located. My preliminary report on the parasite is in *Proc. Hawaiian Ent. Soc.* 12(1):20, 1944. DDT is an excellent insecticide for use in controlling this species.

Genus **LOBOPTERA** Brunner, 1865**Loboptera dimidiatipes** (Bolivar) (fig. 43).*Temnopteryx dimidiatipes* Bolivar, 1890:300, pl. 1, fig. 1.*Temnopteryx sakalava* Saussure, 1891:25. Synonymy by Hebard, 1933:121.*Loboptera sakalava* (Saussure), of authors.*Loboptera extranea* Perkins, 1899:6; type series from Maui and Hawaii. Synonymy by Hebard, 1922:331 and 1933:121.

Figured by Williams, 1931:51.

Kauai, Oahu, Maui, Hawaii.

Immigrant. Africa to Philippines, New Caledonia, Fiji, Samoa, Tahiti, Marquesas. First recorded from Hawaii by Perkins (1899:6).

This is a brachypterous species.

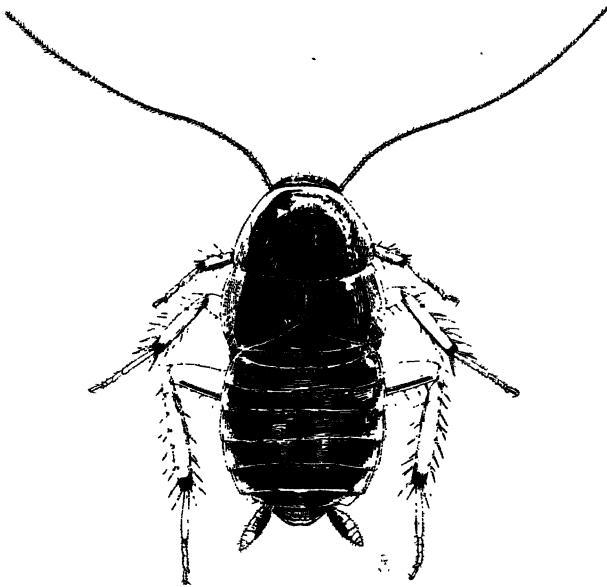


Figure 43—*Lobopectera dimidiatipes* (Bolivar). (From the original drawing by Williams, 1931.)



Figure 44—*Cutilia soror* (Brunner).

Subfamily BLATTINAE

Genus **CUTILIA** Stål, 1877

Cutilia soror (Brunner) (figs. 36, c; 44).

Polyzosteria soror Brunner, 1865:219.

Ootheca figured by Williams, 1931, pl. 2, fig. 1.

Kauai, Oahu, Molokai, Lanai, Hawaii, Kahoolawe, Nihoa, Laysan, Kure (Ocean).

Immigrant. Widespread in Oceania. Formosa, Amboina, Ceram, New Caledonia, Loyalty Islands, Fiji, Tonga, Samoa, Ellice Islands, Johnston Island, Wake Island, Society Islands, Marquesas. First recorded from Hawaii by Perkins (1899:6).

Common in bunch grass in drier regions; in decaying logs. Adults brachypterous.

Parasites: *Dolichurus stantoni* Ashmead (Hymenoptera: Ampulicidae), on nymphs; *Evania appendigaster* (Linnaeus) (Hymenoptera: Evaniidae), on eggs.



Figure 45—*Neostylopyga rhombifolia* (Stoll), the harlequin cockroach, male.

Genus **NEOSTYLOPYGA** Shelford, 1911

Neostylopyga rhombifolia (Stoll) (fig. 45).

Blatta rhombifolia Stoll, 1813:5, pl. 3, fig. 13.

Stylopyga decorata Brunner, 1865:224.

The harlequin cockroach.

Oahu, Kahoolawe.

Immigrant. An Indo-Malayan species, now tropicopolitan. First recorded from Hawaii by Bormans (1882).

Parasite: *Ampulex compressa* (Fabricius) (Hymenoptera: Ampulicidae) on the adults.

This is another flightless cockroach.

Genus **PERIPLANETA** Burmeister, 1838

Hawaiian name: "elehu-kikeke"

These cockroaches may be controlled by the use of DDT dusts and sprays.

Periplaneta americana (Linnaeus) (figs. 36, b; 46).

Blatta americana Linnaeus, 1758:424.

Figured by Williams, 1931:52; ootheca, pl. 2, fig. 2.

The American cockroach.



Figure 46—The three species of *Periplaneta* established in Hawaii: *P. americana* (Linnaeus), left; *P. australasiae* (Fabricius), middle; *P. brunnea* Burmeister carrying nearly completed ootheca, right. (Not to same scale.)

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii, Nihoa, Necker, French Frigate Shoal, Laysan, Midway.

Immigrant. Cosmopolitan. A native of tropical Africa. First recorded from Hawaii by Bormans in 1882.

Hostplants: blossoms of *Canna* and *Tribulus*.

Parasites: *Evania appendigaster* (Linnaeus) and *Evania sericea* Cameron (Hymenoptera: Evaniidae), on the eggs; *Ampulex compressa* (Fabricius) (Hymenoptera: Ampulicidae), on nymphs and adults.

This species is a household nuisance.

Periplaneta australasiae (Fabricius) (figs. 36, a; 46).

Blatta australasiae Fabricius, 1775:271.

Williams, 1931; pl. 2, fig. 3, ootheca.

The Australian cockroach.

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii, Nihoa, Kure (Ocean).

Immigrant. A tropical African species, now tropicopolitan. Australia, Fiji, Gilbert Islands, Samoa, Tahiti, Marquesas, Tuamotus, Easter Island, Galapagos. First recorded from Hawaii by Perkins (1899:7).

Hostplants: *Pritchardia*, *Sida*.

Parasites: *Evania appendigaster* (Linnaeus) and *Evania sericea* Cameron (Hymenoptera: Evaniidae), in the oothecae; *Ampulex compressa* (Fabricius), on the nymphs and adults.

This is another pest species. I have found these roaches breeding by scores in rock piles accompanied by large numbers of *Scolopendra* centipedes and large spiders (*Heteropoda regia*) which probably prey upon the roaches.

Periplaneta brunnea Burmeister (fig. 46).

Periplaneta brunnea Burmeister, 1838:502.

Periplaneta truncata Brunner, in Krauss, 1892:165.

Periplaneta ignota Shaw, 1925:205.

Oahu.

Immigrant. Tropicopolitan; originally a tropical African form. Australia, New Britain, New Caledonia, Loyalty Islands, New Hebrides, Tonga, Marquesas, tropical America. First recorded from Hawaii by Swezey in 1929.

This is the least common of our *Periplaneta* species.

Subfamily PANCHLORINAE

Genus **LEUCOPHAEA** Brunner, 1865

Leucophaea maderae (Fabricius) (fig. 47).

Blatta maderae Fabricius, 1793:6.

The Madera (or Madeira) cockroach.

Kauai, Oahu, Molokai, Maui, Hawaii.

Immigrant. A native of West Africa, but now nearly tropicopolitan. Fiji, Philippines, Java. First found in the islands at Molokai in 1896 or 1897 by Schauinsland.

Largest of the Hawaiian cockroaches (40–50 mm. long) ; said to be ovoviviparous. Bionomical studies by Illingworth (1915:137).



Figure 47—*Leucophaea maderae* (Fabricius), nymph and adult. (Not to same scale.)

Genus **NAUPHOETA** Burmeister, 1838

Nauphoeta cinerea (Olivier) (fig. 48).

Blatta cinerea Olivier, 1789:314.

Nauphoeta bivittata Burmeister, 1838:508.

The cinereous cockroach.

Oahu, Hawaii.

Immigrant. First recorded from Hawaii by Perkins (1899:7). Tropicopolitan ; an East African species first described from Mauritius. Malaya, Sumatra, Philippines, Australia, New Caledonia.

It is ovoviviparous. Illingworth (1942:169-170) reported finding, by dissection, 28 to 40 eggs in gravid females. He also reported that the species kills and eats the cypress roach (*Diploptera*), that it is omnivorous and that heavy infestations were observed in prepared poultry feed.

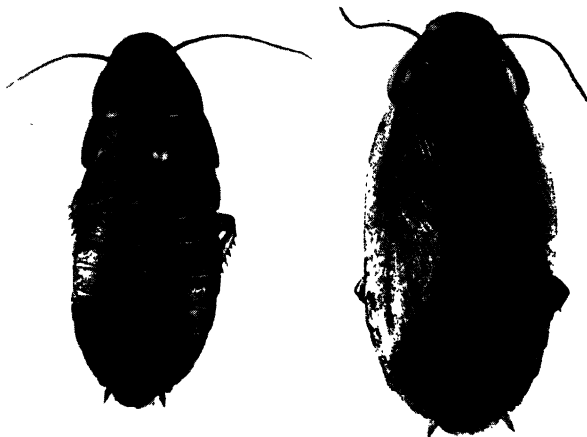


Figure 48—*Nauphoeta cinerea* (Olivier), the cinereous cockroach, nymph and adult.

Genus **PYCNOSCELUS** Scudder, 1862

Pycnoscelus surinamensis (Linnaeus) (fig. 49).

Blatta surinamensis Linnaeus, 1767:687.

Blatta punctata Eschscholtz, 1822:86; described from Hawaii.

Williams, 1931:51, figures nymph and adult.

The burrowing, Surinam or bicolored cockroach.

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii, Nihoa, French Frigate Shoal, Pearl and Hermes Reef.

Immigrant. The first cockroach recorded by name from Hawaii (Eschscholtz: 1822). An Oriental species, now tropicopolitan. Indo-Pacific, Society Islands, Caroline Islands, Fiji, Tonga, Samoa, Gilbert Islands, Johnston Island, New Caledonia, Loyalty Islands, New Hebrides, Marquesas, Tuamotus, Galapagos.

Hostplants: blossoms of *Tribulus*; reported feeding at roots of pineapples, and unconfirmed reports of damage to underground parts of some other plants. Hoffman (1927) reports damage to rose roots and to potato tubers in Haiti. It acts more like a scavenger than a regular feeder on fresh plant material, however.

Ovoviviparous; reported to be parthenogenetic in some localities; abundant in loose soil, under stones, under boards and other objects lying on the ground, in trash and similar situations, in drier areas especially; nymphal period, 10 months.

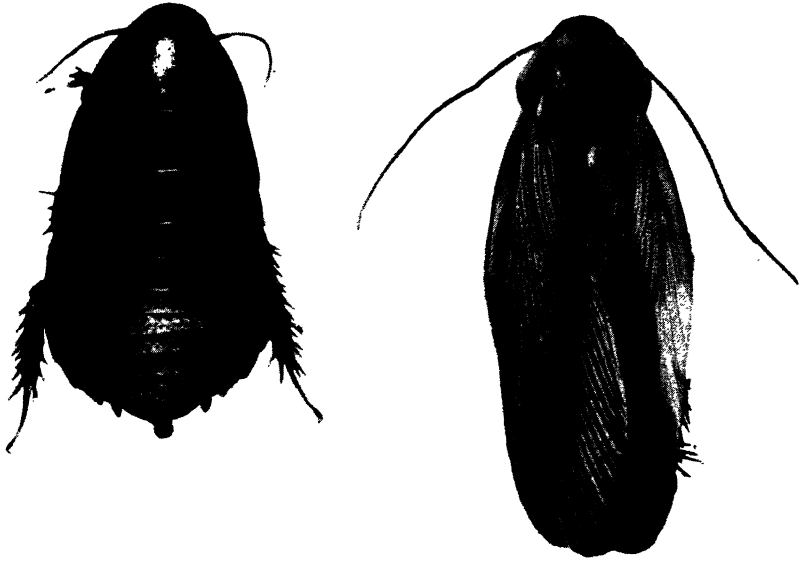


Figure 49—*Pycnoscelus surinamensis* (Linnaeus), the burrowing cockroach, nymph and adult.

Parasites: none recorded in Hawaii, but *Sarcophaga sternodontis* (Townsend) (= *lambeus* Weideman) (Diptera) might be introduced from the West Indies to aid in control. In the West Indies, Hoffman (1927) found 40 percent of the roaches parasitized. The parasite also attacks a host of other insects including Scarabaeidae, Pentatomidae and Lepidoptera.

Predators: sparrows, mynah birds, barnyard fowls, toads (at times, 40–50 percent of the diet of the imported toad, *Bufo marinus*, is reported to be this roach).

Veterinary importance: This species is an intermediate host of Manson's eye worm of poultry. Chickens should be kept off the ground to prevent their eating the roaches and becoming parasitized. The worms have been found in the legs, abdomens and thoraxes of the cockroaches.

Control: This roach usually becomes so abundant in poultry yards that control is recommended. Alicata (1938) reports that "butyric fermentation baits were in some cases found effective in capturing up to about 700 roaches in a single trap. Each trap consisted of a wide-mouthed glass jar about 9 inches high and 5 inches wide, which contained the bait. This trap was set in the ground so that the mouth opening of the jar was at a level with the surface of the ground." Carbon bisulfide and a spray of Diesel oil have been used successfully. Cleanliness will go far toward keeping the roach populations down, but accumulations of manure and debris will encourage the building up of large numbers of roaches. DDT sprays and dusts are recommended for control.

Genus **DIPLOPTERA** Saussure, 1864

Eleutheroda Brunner, 1865.

Diploptera dytiscoides (Serville) (fig. 50).

Blatta dytiscoides Serville, 1839:102.

Eleutheroda dytiscoides (Serville) Brunner, 1895:893.

Chopard, 1929:22, fig. 14. Williams, 1931, figs. 7, 12.

The cypress cockroach.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii.

Immigrant. Widespread in the Indo-Pacific, India, Ceylon, Singapore, Australia, Fiji, Samoa, Society Islands, Marquesas, Easter Island. First reported from Hawaii by Bormans in 1882.

Hostplants: *Cupressus macrocarpa*, *Casuarina*, *Cryptomeria*, *Citrus*, geraniums, *Acacia farnesiana* pods, mango fruits, orange fruits, papaya fruits; damages cypress, *Prosopis*, lime and some other plants by girdling and killing the twigs and limbs. The dead, drying, brown branches are often conspicuous on cypress trees and cause considerable concern to garden lovers.

Control: It is not an easy insect to control, but the use of stomach poison sprays and poison baits such as phosphorus paste on bread placed in protected containers

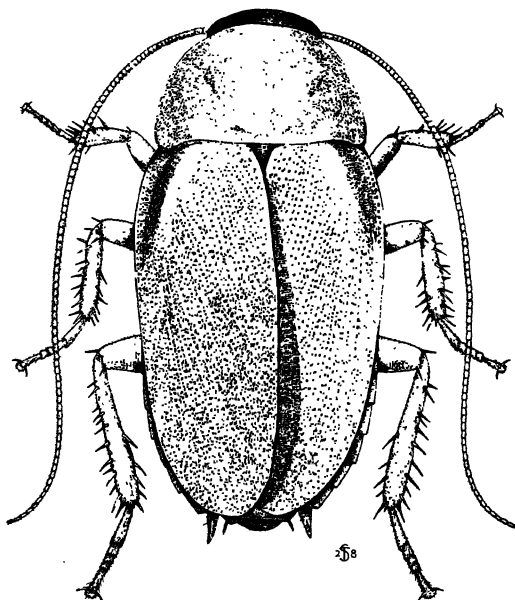


Figure 50—*Diploptera dytiscoides* (Serville), the cypress cockroach. (From Twigg-Smith's original drawing for Williams, 1931.)

on attacked plants are possible measures. Dusting infested trees with sodium fluoride powder or DDT and reducing their numbers by beating them off plants after dark and destroying the catch will give some aid. Dusting or spraying must be repeated frequently if control is to be attained, however.

Predators: toads and geckoes.

Ovoviviparous: embryological studies by Hagan (1939:264).

Subfamily CORYDIINAE

Genus **EUTHYRRHAPHA** Burmeister, 1838

Euthyrrhapha pacifica (Coquebert) (figs. 36, d; 51).

Blatta pacifica Coquebert, 1804:91, pl. 21, fig. 1.

Williams, 1931, pl. 2, fig. 5, ootheca.

The Pacific cockroach.

Kauai, Oahu, Maui, Hawaii.

Immigrant. First recorded from Hawaii by Bormans in 1882. Almost tropicopolitan.

This handsome little species is diurnal in habit and may frequently be seen in its rapid, erratic flight in the fields of drier areas. Its actions are not "typically" cockroach-like, and it is not infrequently confused with the beetles by laymen.

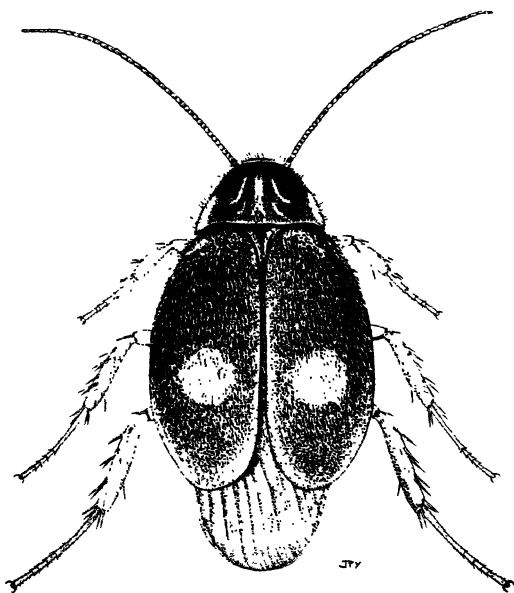


Figure 51—*Euthyrrhapha pacifica* (Coquebert), the Pacific cockroach. (From Yamamoto's original drawing for Williams, 1931.)

Genus **HOLOCOMPSA** Burmeister, 1838

Holocompsa fulva (Burmeister) (fig. 52).

Corydia fulva Burmeister, 1838:492.

Hawaii.

Immigrant. Ethiopian. First recorded from Hawaii by Illingworth (1916:254), but Perkins found it common at Hilo in August, 1900.

This is the smallest cockroach found in Hawaii, for it is only about 5 mm. in length. It is not often collected here. The brachypterous females produce tiny oothecae (about 2 mm. long).



Figure 52—*Holocompsa fulva* (Burmeister).

In addition to these species, Bormans (1882) recorded *Oniscosoma pallida* Brunner (1865:343) from material supposedly collected by Blackburn on Haleakala, Maui. This species has not been found since in Hawaii and is, therefore, omitted from this list. The record might have been based upon a mislabeled or misidentified specimen.

Suborder GRESSORIA (Fieber)

Family MANTIDAE Saussure, 1869

Mantids, Praying Mantids, Soothsayers

Large, comparatively slow-moving, elongate insects; head exposed, mobile, vertical, large, broader than long, flexibly attached to prothorax by a short neck; antennae inserted between the eyes, filiform, less than one-half as long as body,

segments multitudinous; compound eyes large, prominent, fronto-lateral, sub-hemispherical; with three ocelli on a triangular prominence above and between antennal bases; mandibles large, dentate; maxillary palpi five-segmented; labial palpi three-segmented; pronotum longer than broad or greatly elongate and several times longer than broad, neck-like; fore wings in our species with only anterior margins tegmenized, elsewhere membranous and with well-defined venation; hind wings well-developed; abdomen with 10 tergites, nine ventrites in males, seven ventrites in females, but the first ventrite usually reduced so that only eight or six ventrites are distinct, cerci segmented, male with styli; ovipositor wanting; legs with anterior pair greatly modified, raptorial; fore coxae elongate, femora-like; fore femora elongate, with an armature of teeth along ventral margin; fore tibiae shorter than femora, also armed below, capable of closing on femora, strongly uncinat; mid and hind legs not so modified, coxae normal, femora and tibiae elongate, slender; tarsi five-segmented, first four segments with pulvilli; paired tarsal claws without arolia between them; oviparous, eggs deposited in oothecae.

There are three species of Mantidae found in Hawaii, but all are immigrants, and each belongs to a different genus.

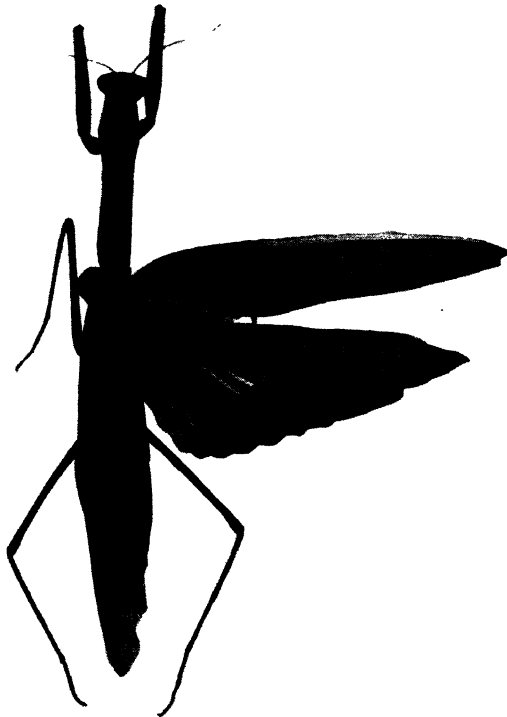


Figure 53—*Tenodera angustipennis* Saussure, a praying mantid.

Some of the most curious members of the insect world are found in the mantid family, but the species found in Hawaii are neither greatly specialized nor unusual. The group is essentially tropical.

At egg laying, the female produces a foamy substance which surrounds the eggs, dries on exposure and forms the ootheca. The eggs are so deposited and the "foam" so controlled and manipulated by the end of the abdomen and the apices of the wings that the end product is a well-formed, characteristic, hardened papier maché-like ootheca in which the eggs are enclosed in more or less symmetrical chambers. The oothecae are fastened to limbs, twigs, posts and other objects.



Figure 54—Ootheca of *Tenodera angustipennis* Saussure.

Mantids are voracious insect tigers, and their predaceous habits place them among our beneficial insects. Hadden (1927) has listed 29 species in five orders of insects seen by him to be eaten by one of our mantids (*Tenodera*). They attack nearly all kinds of arthropods that come their way. Their common name is derived from the attitude they assume when at rest or when awaiting some hapless insect that may chance within striking distance: the fore legs are so held as to make the insect look as if it were praying instead of preying.

The coloration of our species makes them inconspicuous among the foliage on which they live.

In many regions, mantids are considered sacred, are worshiped, or are looked upon with awe, and many local myths and much superstition is connected with them.

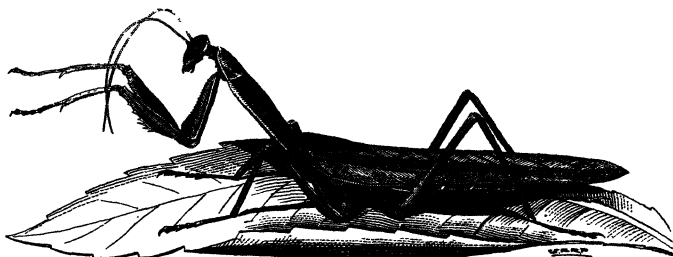


Figure 55—*Tenodera angustipennis* Saussure, natural size, awaiting the approach of prey. (After Kirkaldy, 1909.)

KEY TO THE MANTIDS FOUND IN HAWAII

1. Pronotum not more than twice as long as broad, broadest at apex, apex broadly and only slightly arcuate, subtruncate; length about 40 mm.; subfamily Eremiaphilinae.....
.....**Orthodera ministralis** (Fabricius).
Pronotum slightly more than twice as long as broad to more than four times as long as broad, broadest at a distance behind apex above insertion of coxae, apex conspicuously rounded; length 65-90 mm.; subfamily Mantinae..... 2
2. Pronotum about four times or more than four times as long as broad; length of insect 80-90 mm.....
.....**Tenodera angustipennis** Saussure.
Pronotum slightly more than twice as long as broad; length of insect less than 70 mm.....**Hierodula patellifera** (Serville).

Subfamily EREMIAPHILINAE

Genus **ORTHODERA** Burmeister, 1838

Orthodera ministralis (Fabricius).

Mantis ministralis Fabricius, 1775:277.

Orthodera prasina Burmeister, 1838:530.

Kauai.

Immigrant. Australia. First recorded in Hawaii from Kauai by Perkins as "introduced with fruit trees" (1899:7).

Prey: *Coelophora inaequalis* (Fabricius) (Coleoptera: Coccinellidae) and many other kinds of insects not yet recorded in our literature.

I have seen only a few examples of this species, and none has been in satisfactory condition to photograph.

Subfamily MANTINAE

Genus **TENODERA** Burmeister, 1838

Tenodera angustipennis Saussure (figs. 53, 54, 55).

Tenodera angustipennis Saussure, 1869:69.

This species has been called *Tenodera sinensis* Saussure and *Paratenodera sinensis* (Saussure) in Hawaii by error of identification.

Jones, 1933:1, pl. 1, figures adult and egg mass. Rehn, 1933:4, gives differences between *T. angustipennis* and *T. sinensis*.

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii.

Immigrant. China, Japan, Java, North America (recent immigrant). First found on the island of Hawaii in 1900, according to Perkins (1910:689).

Introduced from Hawaii to Oahu; established on Oahu in 1918. May produce several oothecae at 10-day intervals, each ootheca containing up to about 300 eggs. See Hadden (1927) for list of prey.

Parasites: *Podagrion mantis* Ashmead (Hymenoptera: Calliomidae) and *Cerambycobius cushmani* Crawford (Hymenoptera: Eupelmidae).

Predators: cardinal birds.

Genus **HIERODULA** Burmeister, 1838

Hierodula patellifera (Serville) (fig. 56).

Mantis patellifera Serville, 1839:184.

Kauai.

Immigrant. Java, Philippines. First collected by Swezey on Kauai in 1924. The males collected here are brown and the females green.



Figure 56—*Hierodula patellifera* (Serville).

Suborder SALTATORIA (Latreille, 1817)

Family ACRIDIDAE von Siebold, 1848

Acridioidea

Acridiidae

Locustidae

Grasshoppers, Locusts, Short-horned Grasshoppers

Leaping insects; head exposed, face vertical or almost horizontal; antennae filiform, moniliform or setaceous, inserted between the eyes, not longer than head and thorax in our species; with less than 25 segments, segments distinct; compound eyes large; three ocelli present, in our species one situated on the mid-line of the face below antennae, and one on either side above antennae; mandibles large, prominent, dentate; maxillary palpi five-segmented; labial palpi three-segmented; pronotum saddle-like; tegmina and wings, when at rest, folded in such a way as to protect partially the sides as well as dorsum of abdomen and fitting together in a vertical plane at apex beyond end of abdomen; abdomen 11-segmented, usually with nine completely visible tergites, males with nine entire ventrites, females with seven entire ventrites; cerci not distinctly segmented; ovipositor short but visible,

composed of four sclerites; tympana large, situated on sides of first abdominal segment; fore and middle legs short, similar; hind femora greatly enlarged for leaping; hind tibiae elongate; tarsi three-segmented, first two segments with pulvilli; claws divergent; arolium present; oviparous, eggs deposited in clusters in soil; diurnal insects.

Fossil acridids have been found in Tertiary (Oligocene, Miocene, Pleistocene) and Recent horizons.

Only three grasshoppers are found in Hawaii; all of them are immigrants.

Most of us are exposed to grasshoppers early in our entomological careers, for these insects have been used in beginning courses in zoology and entomology for several generations.

A number of the world's worst insect pests are included in this family. And it is to this family that the migratory or plague locust of historical and modern times belongs. The student is referred to some standard text for detailed discussions and guides to the literature if he wishes to study the extra-Hawaiian members of the group in detail (Uvarov, 1928, gives detailed information on some of the most economically important species together with general details).

Grasshoppers are vegetarians, and we in Hawaii are fortunate that the three species we have are not such bad pests as they might be. Our species do cause some damage to a number of crops and garden plants, but, broadly speaking, they are insects of weeds and wayside grasses and do comparatively small amounts of damage when compared with their notoriously destructive allies elsewhere.

Grasshoppers may be controlled by the use of stomach poison sprays, or poison baits. A number of parasites and predators act to control the populations of our species. Known parasites and predators from other countries might be introduced to Hawaii in the future to restrict further the development of the Hawaiian forms.

At egg laying, the female forms a cavity in the soil by use of her abdomen. The eggs are then deposited in the hole in a frothy substance similar to that from which the oothecae of the mantids is composed.

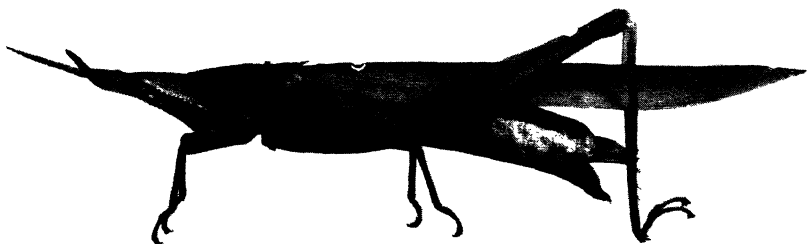


Figure 57—*Atractomorpha ambigua* Bolivar, the slant-faced grasshopper, female.

KEY TO THE SUBFAMILIES FOUND IN HAWAII

1. Front of head oblique, more nearly horizontal than vertical, meeting top of head at an acute angle, head pointed and produced beyond eyes; clypeus not below eyes, but at a distance behind a line drawn perpendicular to them....**Pyrgomorphinae.**
2. Front of head more nearly vertical than horizontal, rounded into top of head; clypeus directly below eyes.....**Cyrtacanthacridinae.**

Subfamily PYRGOMORPHINAE

The Slant-faced Locusts

Genus **ATRACTOMORPHA** Saussure, 1861**Atractomorpha ambigua** Bolivar (fig. 57).

Atractomorpha ambigua Bolivar, 1905:209.

Called *A. crenaticeps* Blanchard, in earlier Hawaiian literature because of an error in determination. Williams, 1931:62, fig. 16.

The slant-faced grasshopper, pink-winged grasshopper, pink-winged tryxalid. Kauai, Oahu, Molokai, Maui, Hawaii.

Immigrant. China, Japan, Australia. First recorded from Hawaii (Oahu) by Kotinsky in 1906, but known to have been found here in 1900. (A specimen in Perkins' collection at Bishop Museum is noted by Perkins as the "first caught specimen Govt. nursery in 1900.") First recorded on Kauai by Swezey in 1918.

Hostplants: *Scaevola chamissoniana*, pineapple, broccoli, celery, garden beans, Chinese and other cabbage, New Zealand spinach, potato, many kinds of weeds and garden plants.

Predators: English sparrow, Brazilian cardinal.

Bionomical studies by Swezey (1907:106). Dichromatic, gray or green; eggs laid in December and January; egg mass in soil, cylindrical, 4 × 12 mm., contains 27-38 dull yellowish eggs 1 × 4 mm.; egg stage 47-49 days; 5-6 molts; instars 10-20 days each; life cycle 5 months.

Subfamily CYRTACANTHACRIDINAE

The Spine-breasted Locusts

KEY TO THE GENERA ESTABLISHED IN HAWAII

1. Adults fully winged**Oxya** Serville.
2. Adults without wings.....**Paraideмона** Brunner.

Genus **OXYA** Serville, 1831

Oxya chinensis (Thunberg) (figs. 58; 59, 1-4).

Gryllus chinensis Thunberg, 1815:253.

Listed in earlier Hawaiian literature as *Oxya velox* (Fabricius) because of error of identification. Willemse, 1925:49, figs. 54-57. Swezey, 1926:378, fig. 1, adult, egg mass, damage to sugarcane.

The Chinese grasshopper.

Kauai, Oahu, Maui, Hawaii.

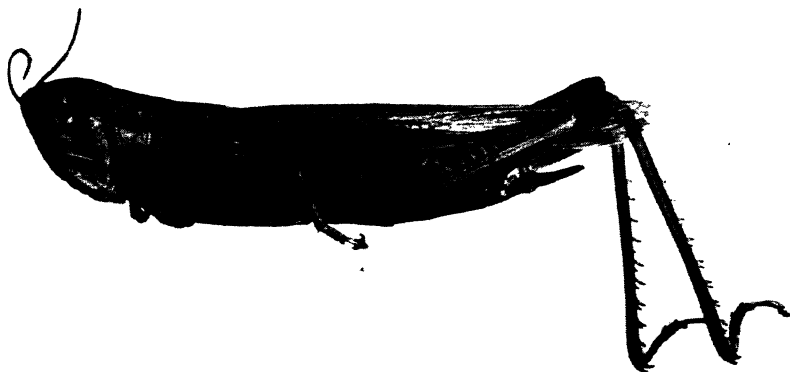


Figure 58—*Oxya chinensis* (Thunberg), the Chinese grasshopper, female.

Immigrant. Widespread in India, Burma, Ceylon, Siam, China, Japan, Mauritius, Malay Peninsula, Sumatra, Borneo, Java, Philippines, Moluccas, Celebes, New Britain, Australia. Found in Hawaii before 1892; first recorded by Brunner (1895:893). Known from Kauai and Oahu in 1897; first found on Maui in 1918 and on Hawaii in 1925.

Hostplants: grasses, Job's tears, nutgrass, *Panicum purpurascens*, *Passiflora*, pineapple, potato, rice, sugarcane (produces ragged leaves and may cause minor checking of growth; occasionally does severe local damage, especially adjacent to rich patches of nutgrass, where populations build up).

Parasites: *Tachysphex fuscus* Fox (Hymenoptera: Sphecidae) on nymphs; *Scelio pembertonii* Timberlake (Hymenoptera: Scelionidae) on eggs; a *Gordius* roundworm. Pemberton made a trip to the Malay Peninsula in 1930-31 to search for parasites and introduced the *Scelio*.

Predators: sparrows, mynah birds.

Bionomical studies by Swezey, 1926:378. Egg masses contain about 20 eggs, as many as three batches per female, usual incubation period six weeks, but delayed hatching up to 277 days recorded; seven molts; 10-16-day instars; nymphal period 6-10 weeks; adults live two to three months; two broods per year.

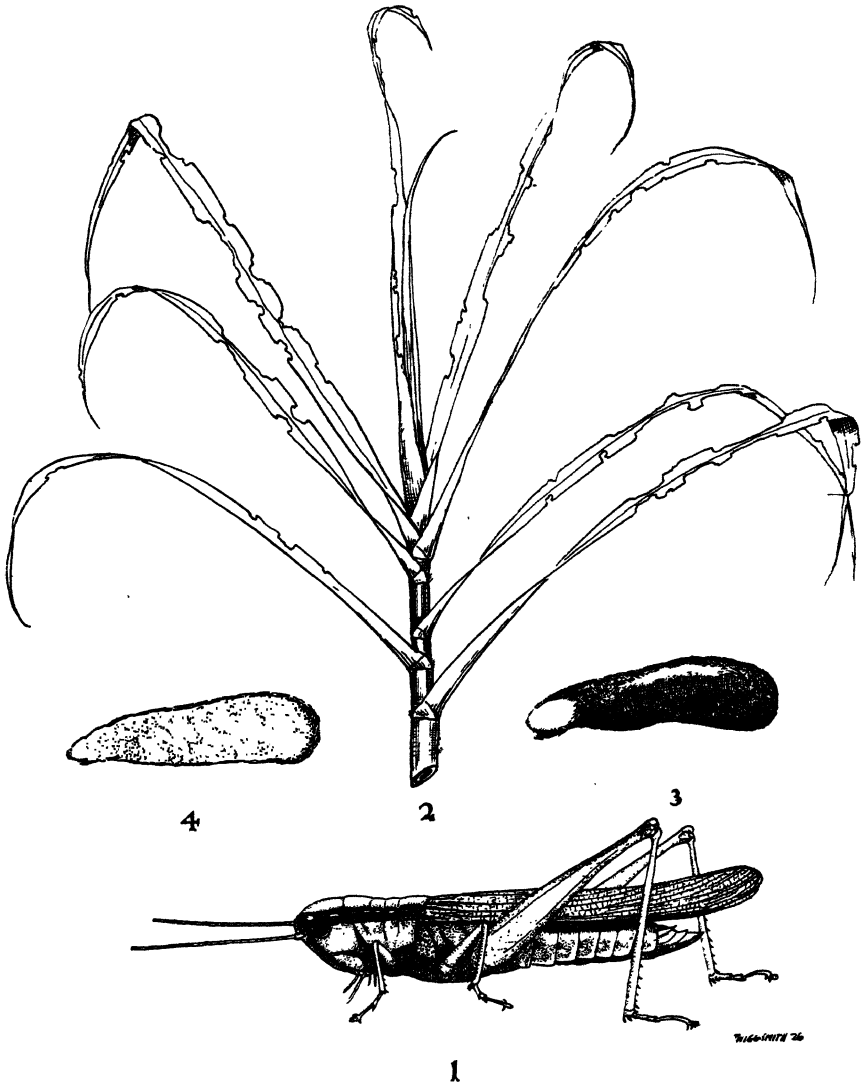


Figure 59—*Oxya chinensis* (Thunberg), the Chinese grasshopper. 1, adult female; 2, typical damage done to the leaves of a young sugarcane shoot; 3, egg mass; 4, egg mass sectioned to show the enclosed eggs. (After Swezey, 1926.)

Genus **PARAIDEMONA** Brunner, 1893

This is a northern Mexican and Texas genus.

Paraideмона mimica Scudder (fig. 60).

Paraideмона mimica Scudder, 1898:43, pl. 3, fig. 10.

Oahu.

Immigrant. Described from Texas. First discovered at Hickam airfield, Honolulu, in July, 1945, by C. E. Pemberton.

Hostplants: grasses.

This species has become established through the importation of materials of war, and it will bear close watching.

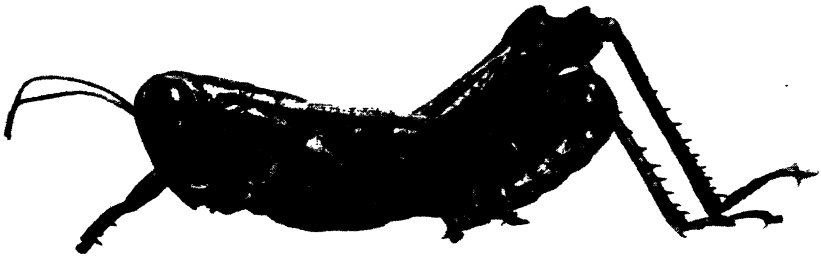


Figure 60—*Paraideмона mimica* Scudder, male.

Family TETTIGONIIDAE Karny, 1903

Locustidae Burmeister, 1838.

Phasgonuridae.

Katydids, Longhorned Grasshoppers

Leaping insects; head exposed, prominent; antennae elongate, longer than body, filiform, multisegmented, inserted between eyes; compound eyes large; ocelli absent; mandibles large, prominent, dentate; maxillary palpi five-segmented; labial palpi three-segmented; pronotum large, saddle-like; tegmina and wings fully developed or brachypterous, held roof-like over after-body and projecting far beyond apex of abdomen when fully developed; tegmina usually leaf-like in appearance, not heavily sclerotized; hind wings, when fully developed for flight, projecting a short distance beyond apices of tegmina; bases of tegmina in male modified to form stridulating organs; abdomen 10-segmented, with nine complete tergites visible; males with nine complete ventrites, the ninth enlarged and modified, female with seven; ovipositor conspicuous, long, strongly developed, heavily sclerotized, blade-like, composed of six compactly placed sclerites; male genitalia large, conspicuous (*Phaneropterinae* with two elongate, ventral processes somewhat resembling an ovi-

positor); cerci not segmented; hind legs with femora and tibiae elongate, much longer than others, hind femora modified for leaping; fore tibiae bearing tympanal organs just below articulation with femora; tarsi four-segmented, first three segments with pulvilli; tarsal claws divergent or divaricate, with empodia; oviparous, eggs inserted in plant tissues; nocturnal insects of herbivorous, omnivorous or predaceous habit.



Figure 61—*Elimaea punctifera* (Walker), the narrow-winged katydid, female.

There have been 16 katydids and longhorned grasshoppers recorded from Hawaii. The family reaches its greatest diversity in the tropics, and there are more than 7,000 species described from the world. The Hawaiian fauna contains two groups, one immigrant with four species in four genera, the other endemic with 11 species and one variety in two genera, both of which are endemic.

The katydids are well-known insect musicians, and their stridulated songs have been the subject of much study and comment for ages. Stridulation is a male attribute and is accomplished by rubbing the specialized bases of the tegmina together. The underside of the stridulating organ on the left tegmen is armed with small denticles which are rubbed across a drum-like membrane on the right tegmen to produce the characteristic song or chirping of the species. Our Phaneropterinae are our best songsters among the Tettigoniidae.

In other countries large and queer forms are found, and some apterous, pale, blind species dwell in perpetual darkness and make up a dominant part of the faunas of certain limestone caverns.

The Hawaiian katydids are all found on small plants, shrubs or trees. None of them is terrestrial. *Banza* has reduced wings and does not fly, but the species of the other genera are active fliers.

The large, blade-like ovipositors of the females enable them to make incisions in the stems of many kinds of plants into which the eggs are inserted. This habit causes some injury to certain plants.

The Hawaiian species include no serious pests, but damage of a minor sort, or of restricted serious nature, is on occasion caused by some of the adventitious species. Stomach poison sprays will aid in the control of katydids when they are found causing significant damage. At least one of our immigrant species (*Xiphidiopsis*) is more beneficial than detrimental, for it prefers an insect diet.

A number of predators and parasites attack katydids, and those found in Hawaii are listed in the text beneath the species headings.

KEY TO THE SUBFAMILIES OF TETTIGONIIDAE FOUND IN HAWAII

1. Prosternum without a pair of long sharp spines..... 2
 Prosternum with a pair of distinct spines..... 3
- 2(1). Fore tibiae with spines along inner edge shorter than breadth
 of tibia at middle; tympanum enclosed, opening through a
 longitudinal, outward-facing slit on either side of tibia, or
 at least enclosed on one side..... **Phaneropterinae.**
 Fore tibiae with long, strong, prominent spines along lower
 edge which are obviously longer than breadth of tibia at
 middle; tympanum entirely open, oval and "window-like"
 **Listrocelinae.**
- 3(1). Fore and/or mid femora with at least a few stout, tooth-like
 spines along anterior ventral margin toward apex, hind
 femora with similar, more numerous spines along both
 inner and outer ventral margins in distal half, but those on
 outer margin less numerous or only a few toward apex;
 distance from a line drawn between anterior edges of eyes
 to apex of fastigium much greater than length of eye, as
 viewed from above (in other words, the fastigium is much
 more protuberant); all but one of our species flightless
 **Copiphorinae.**
 Fore and mid femora without any such spines, hind femora
 with only a few widely spaced spines in a single row; dis-
 tance from fore edges of eyes to apex of fastigium much
 shorter than length of eye..... **Conocephalinae.**

Subfamily PHANEROPTERINAE

KEY TO THE GENERA AND SPECIES FOUND IN HAWAII

1. Broadest part of tegmina obviously narrower than distance be-
 tween metacoxa and top of pronotum; tympanum completely
 and equally enclosed on both faces of tibia.....
 **Elimaea punctifera** (Walker).
2. Broadest part of tegmina about as broad as height of meta-
 thorax from coxa to top of pronotum; tympanum almost
 entirely open on posterior side of tibia.....
 **Holochlora japonica** Brunner.

Genus **ELIMAEA** Stål, 1874

Elimaea punctifera (Walker) (figs. 61, 62).

Phaneroptera punctifera Walker, 1869:342.

Elimaea appendiculata Brunner, 1878:101 (reference not seen).

The narrow-winged katydid.

Oahu, Molokai, Hawaii.

Immigrant. India, Burma, Malay Peninsula, Java, Borneo. First recorded from Hawaii by Bormans (1882).



Figure 62—*Elimaea punctifera* (Walker), the narrow-winged katydid, feeding on a flower bud of hibiscus. (After Williams, 1931.)

Hostplants: *Hibiscus*, young avocado leaves, garden beans, coffee, cotton, *Canna*, *Azalea*. It sometimes causes severe damage by destroying buds of *Hibiscus*, eating *Canna* and other blossoms, and damaging the blossoms of mango.

The eggs are deposited in slits in leaf margins of various plants, in tender young shoots of avocado, in fern fronds or other plants, and some injury may be caused by egg laying.

Parasites: *Anastatus koebelei* Ashmead (Hymenoptera: Encyrtidae), *Ufens elimaee* Timberlake (Hymenoptera: Trichogrammidae), both egg parasites.



Figure 63—*Holochlora japonica* Brunner, the broad-winged katydid, female.

Genus **HOLOCHLORA** Stål, 1873

Holochlora japonica Brunner (figs. 63, 64, 65).

Holochlora japonica Brunner, 1878:181.

Holochlora venosa Stål, 1873:43.

The broad-winged katydid.

Oahu, Kauai.

Immigrant. China, Japan, Sumatra, Java. Established in Hawaii about 1896.

Hostplants: *Hibiscus* (damage severe at times), young mango leaves (sometimes damages the flower clusters), *Canna* and other blossoms.

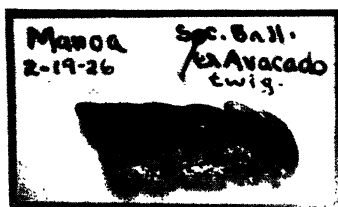


Figure 64—Eggs of *Holochlora japonica* Brunner.

Eggs flat, seed-shaped, as many as one hundred deposited in double rows in slits in young shoots of mango, orange, *Sapindus oahuensis*, *Hibiscus*, *Bougainvillea*, avocado, *Ficus* and cactus. Some injury is done by oviposition.

Parasites: *Zaischnopsis* sp. (see Swezey, 1944:137), *Anastatus koebelei* Ashmead (Hymenoptera: Encyrtidae), *Ufens elimaeae* Timberlake (Hymenoptera: Trichogrammatidae).

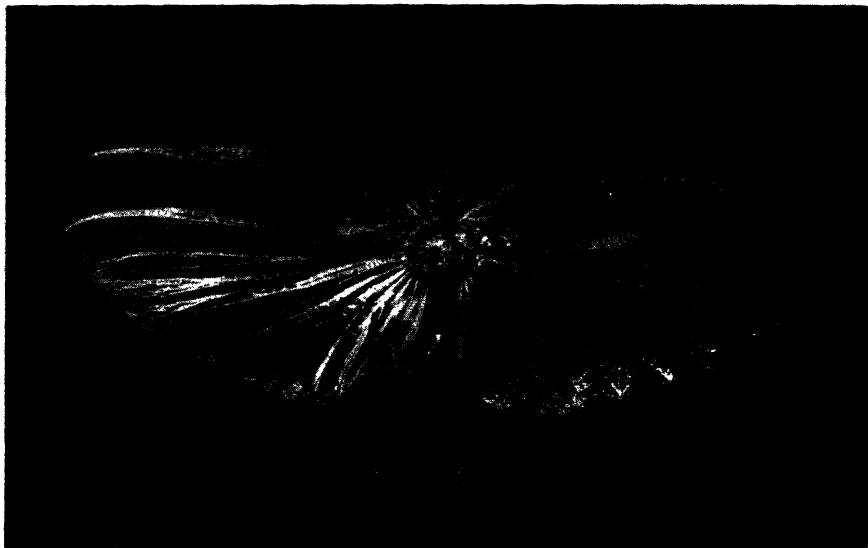


Figure 65—*Holochlora japonica* Brunner, male.

Subfamily COPIPHORINAE

KEY TO THE GENERA FOUND IN HAWAII

1. Tegmina and hind wings fully developed for flight.....
.....**Conocephaloides** Perkins.
2. Tegmina and/or wings greatly reduced, not useful for flight
.....**Banza** Walker.

Genus **CONOCEPHALOIDES** Perkins, 1899:13

This genus was described by Perkins as an endemic genus which formed a connecting link between the native *Banza* and the essentially tropicopolitan *Conocephalus*. He also considered that *Banza* was derived from "some such form as the genus *Conocephaloides*" (1899:2), and later (1913:ccxv) he restated his opinion by saying that *Conocephaloides* was "a form such as one might suppose gave rise to the more remarkable *Banza*." The basis for his description was a single female taken at Olaa, Hawaii, at 2,000 feet elevation. In Kirby's catalog (1906:251), Perkins' species is listed as a synonym of *C. remotus* (Walker), which synonymy Perkins acknowledged without remark (1913:ccxv). In the same reference Perkins said that the species "seems now to be very rare, but was probably once abundant, and has been destroyed by introduced predaceous insects." Considerable collecting has been done in the type locality and no additional specimens have been recovered. Olaa is in the vicinity of homesteads and sugar plantations which were

active in that neighborhood in Perkins' time. This fact, together with the capture of a single specimen, at first led me to believe that it would be found that the insect was an immigrant that failed to become permanently established. In later years Perkins collected a single specimen of *Conocephaloides* near the coast of West Maui and three specimens at 2,000 feet on Lanai. These four specimens are now in the Bishop Museum, and they bear a note by Perkins which reads, "These sp. want comparison as being possibly modified spp. or races. None has the markings of my *hawaiiensis*." No date of collection is given for any of them. The three specimens collected on Lanai were originally preserved in alcohol and are all much faded and somewhat distorted.

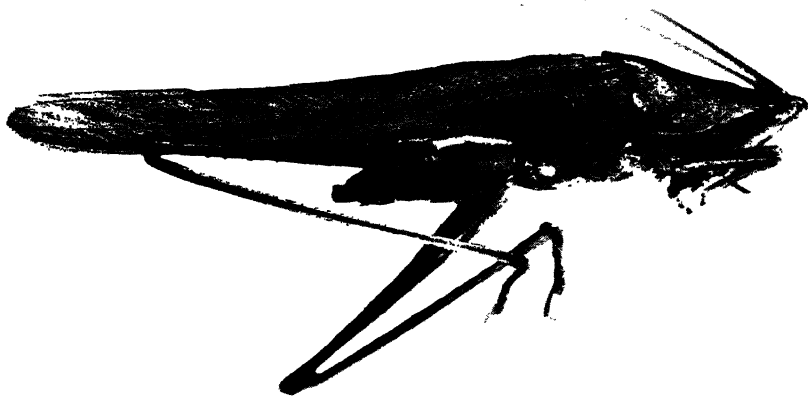


Figure 66—*Conocephaloides remotus* (Walker), male. (This example was taken by Perkins, near the coast on West Maui.)

***Conocephaloides remotus* (Walker) (figs. 66, 67).**

Conocephalus remotus Walker, 1869:326 (reference not seen).

Conocephaloides hawaiiensis Perkins, 1899:13, pl. 1, fig. 8 (type locality: Olaa, Hawaii, 2,000 feet).

Conocephaloides remotus (Walker) Kirby, 1906:251.

Endemic. Maui, Lanai, Hawaii (type locality on Hawaii unknown to me).

The habits of this species are probably such that it might not be collected by casual search during the daytime. Also, there are no resident entomologists in the areas where specimens have been previously collected. I cannot say, therefore, whether or not this species still lives on the adjacent islands of Hawaii, Maui and Lanai, or whether for some unknown reason it has become extinct. It would be worth while to make a special effort to rediscover the species by listening for its



Figure 67—*Conocephaloides remotus* (Walker), a female from Lanai.

buzzing song, perhaps in lush grassy areas at night and tracking down any katydid songsters with the aid of a light.

On the eve of going to press, a fine female example has come to hand. It was collected by T. Miyamoto in a pineapple field on Lanai, January 2, 1941, and it is part of a collection prepared for a University of Hawaii entomology class. This is the first record of the species for about half a century. This example is 50 mm. long (about 2 inches).

Genus **BANZA** Walker, 1870

Microsaga Saussure, 1888:154.

Brachymetopa Redtenbacher, 1891.

This is one of the characteristic endemic genera of the Hawaiian fauna. It probably had its origin in Hawaii from some fully winged ancestral immigrant which was possibly a *Euconocephalus* or a *Euconocephalus*-like insect. The southern and tropical western Pacific areas are richly supplied with such forms which might be ancestral to *Banza*. Hebard (1922:342) said that "*Banza* shows close similarity in general appearance to the genus *Belocephalus*, peculiar to the extreme southeastern United States." However, this similarity is superficial and is not the result of community of origin. I doubt that Hebard wished to convey an opposite impression. *Banza* has much in common with *Euconocephalus* (see the notes under *Conocephaloides*).

All of the species are rather closely allied, and each form is restricted to a single island. The adults are dichromatic, either green or brownish. Some of the species exhibit polychromatism in the nymphal stage. They are nocturnal insects which conceal themselves in foliage during the day and prefer to hide among dead leaves on trees, in dense clusters of foliage, on *Cordyline*, *Freycinetia*, ferns and other plants that give good protection. The eggs are inserted in plant tissues. These

orthopterans are not host-specific and a given species may be found on a number of kinds of plants. The males stridulate at night. They cannot fly, for their wings are atrophied, and the tegmina are greatly reduced; however, they are active jumpers and can often make good their escape even from the most persistent collector. Mynah birds and some of the other introduced birds probably have caused considerable reduction in the numbers of these unusual katydids. At least one *Eupelmus* wasp is a known egg parasite, and Perkins suspected that *Anteris* was also an egg parasite.

It is known that the Hawaiians used to skewer "grasshoppers" on grass stems and roast them over the fire for food many years ago. Could the "grasshoppers" have been *Banza*?

Only Kauai, Oahu and Maui have two species each; each of the other islands has a single species, insofar as we know. The terminalia of the males offer splendid diagnostic morphological characters. Unfortunately, however, there is not a complete set of males and females available to me for study so that a key incorporating the terminalia characters could be prepared. The cerci of the males are greatly modified as clasping organs, and each has two dactyl-like terminal processes. The caudal tergite also displays good specific characters.

Perkins (1899:13) gave a key (in Latin) to the species, and I present here a simple key which will enable the species to be distinguished readily.

KEY TO THE SPECIES OF BANZA

1. Kauai species 2
Not so 3
- 2(1). Tegmina longer than head and pronotum combined.....
.....*affinis* (Perkins).
Tegmina shorter than head and pronotum combined.....
.....*kauaiensis* (Perkins).
- 3(2). Oahu species 4
Not so 5
- 4(3). Tegmina obviously broadly rounded at apex; male with ventral process of each cercus directed more cephalad than transversely, and the dorsal process, directed transversely, crosses over it when viewed from behind. . .*parvula* (Walker).
Tegmina sub-acutely pointed at apex; male with both dorsal and ventral processes of cerci directed more transversely than longitudinally and not crossing one another when viewed from behind.....*unica* (Perkins).
- 5(3). Molokai species*molokaiensis* (Perkins).
Not so 6
- 6(5). Maui species 7
Not so 8
- 7(6). Dorsal processes of male cerci long, stout, erect; ovipositor longer than hind femora.....*brunnea* (Perkins).
Dorsal processes of male cerci small, short, not erect; ovipositor shorter than hind femora.....*mauiensis* (Perkins).

- 8(6). Lanai species; tegmina only about as long as pronotum...
**deplanata** (Brunner).
 Not so; tegmina longer..... 9
- 9(8). Nihoa Island species; tegmina unusually elongate, acuminate**nihoa** Hebard.
 Hawaii species 10
- 10(9). Tibiae normal, slender.....**nitida nitida** (Brunner).
 Tibiae unusually stout.....**nitida crassipes** (Perkins).

Banza affinis (Perkins).

Brachymetopa affinis Perkins, 1899:11.

Endemic. Kauai (type locality: in mountains, 3,000 feet, unique; part of Brunner's original series of *B. deplanata*).

Banza brunnea (Perkins), new combination.

Brachymetopa parvula variety *brunnea* Perkins, 1899:11, pl. 1, fig. 6a.

Brachymetopa parvula Perkins, 1899:11, pl. 1, fig. 6; not *parvula* of Walker, 1869. New synonym.

Brachymetopa brunnea Perkins, Kirby, 1906:254.

Endemic. Maui (type locality: Lahaina, 3,000 feet).

The green and brown forms are not entitled to separate names, hence the above new synonymy.

Banza deplanata (Brunner) (fig. 68).

Brachymetopa deplanata Brunner, 1895:894.

Perkins, 1899:12, limits of species; pl. 1, fig. 7; pl. 2, figs. 3, 3a.

Endemic. Lanai (type locality: 2,000 feet).

Banza kauaiensis (Perkins) (fig. 68).

Brachymetopa kauaiensis Perkins, 1899:10.

Endemic. Kauai (type locality: Makaweli, 2,000 feet).

Banza mauiensis (Perkins) (fig. 69).

Brachymetopa mauiensis Perkins, 1899:12, pl. 1, fig. 5; pl. 2, figs. 4, 4a.

Brachymetopa mauiensis variety *ochracea* Perkins, 1899:12. New synonym.

Endemic. Maui (type locality: Iao Valley, West Maui).

The brown form of this and other species does not deserve a separate name.

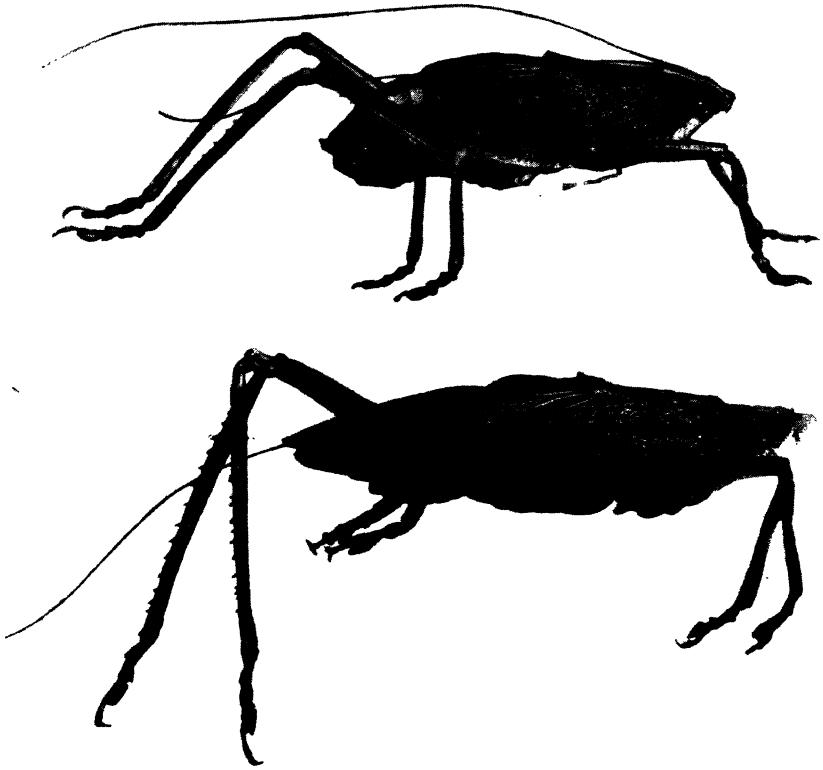


Figure 68—*Banza deplanata* (Brunner), top; *Banza kauaiensis* (Perkins), bottom. Males. (Not to same scale.)

***Banza molokaiensis* (Perkins) (fig. 69).**

Brachymetopa molokaiensis Perkins, 1899:12.

Endemic. Molokai (type locality: 3,000–4,000 feet).

***Banza nihoa* Hebard (fig. 70).**

Banza nihoa Hebard, 1926:83, fig. 9.

Endemic. Nihoa Island (type locality).

Found in bunch grass. The largest species of *Banza*; it has unusually elongated tegmina. It is noteworthy that the largest species of the genus with the greatest tegminal development should be found on the smallest island now inhabited by the genus.

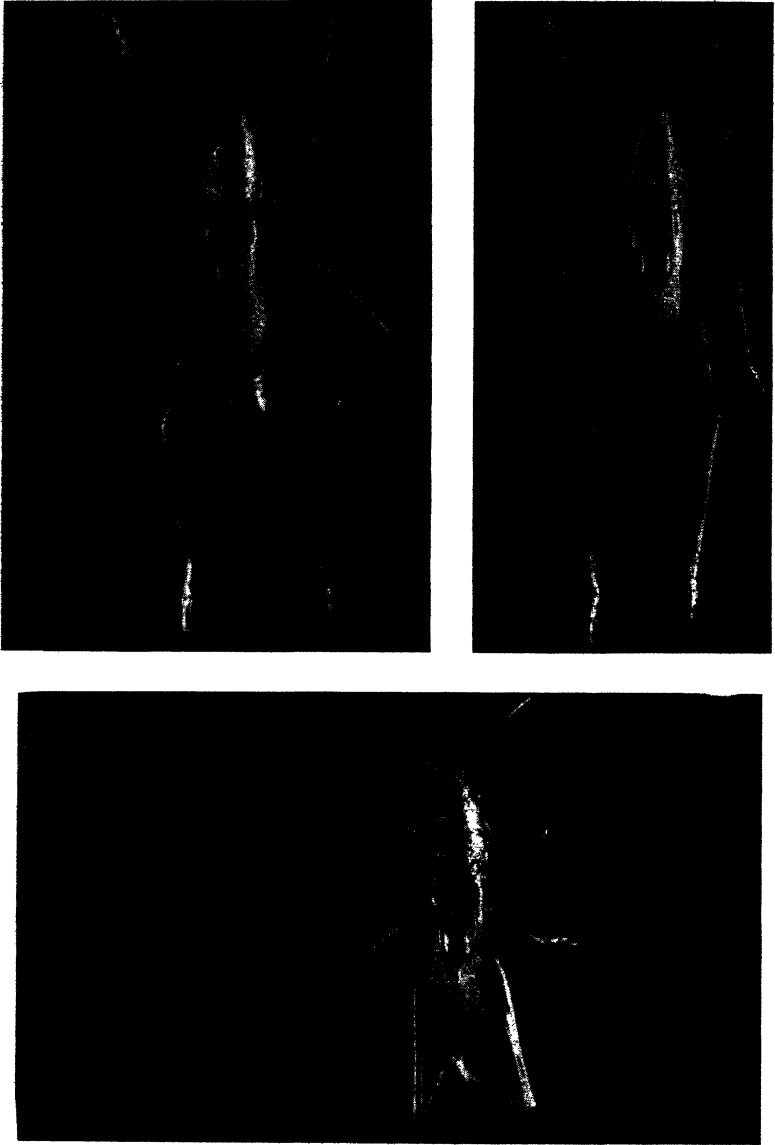


Figure 69—*Banza molokaiensis* (Perkins), left; *Banza mauiensis* (Perkins), right; *Banza unica* (Perkins), bottom. Males. (Not to same scale.).

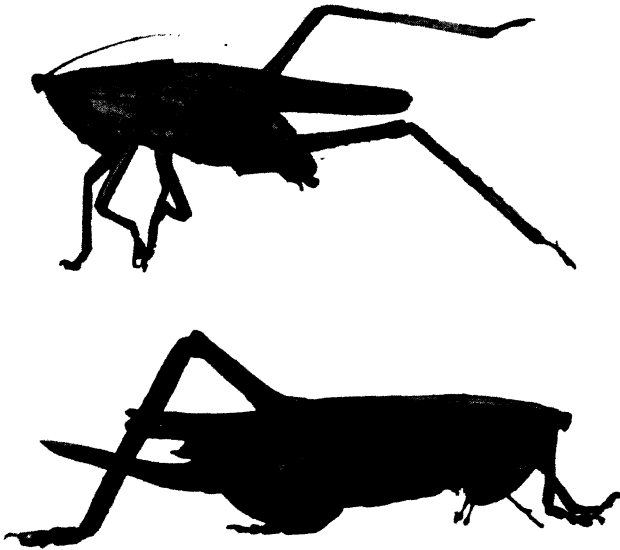


Figure 70—*Banza nihoa* Hebard, male (top), and female. Although this species is found on the smallest island known to support the genus, it is the largest species of the group and has the tegmina more completely developed than those of the other species.

***Banza nitida nitida* (Brunner) (fig. 71).**

Brachymetopa nitida Brunner, 1895:894. Perkins, 1899:9, pl. 1, figs. 3, 3a, 3b; pl. 2, figs. 2, 2a.

Brachymetopa nitida variety *hiloensis* Perkins, 1899:10 (type locality: above Hilo). New synonym.

Brachymetopa nitida variety *punae* Perkins, 1899:10 (type locality: Puna). New synonym.

Endemic. Hawaii (type locality: Kona).

A larger series of specimens assembled since the type series appears to me to show so much intergradation as to make Perkins' varieties untenable.

***Banza nitida crassipes* (Perkins).**

Brachymetopa nitida variety *crassipes* Perkins, 1899:10.

Endemic. Hawaii (type locality: Kilauea, 4,000 feet).

I have not seen this form, but it is apparently quite distinct. Hebard, 1922:344, who has examined specimens agrees with Perkins in considering it a separate form. Perhaps it should be called a subspecies, or it may even be a distinct species.

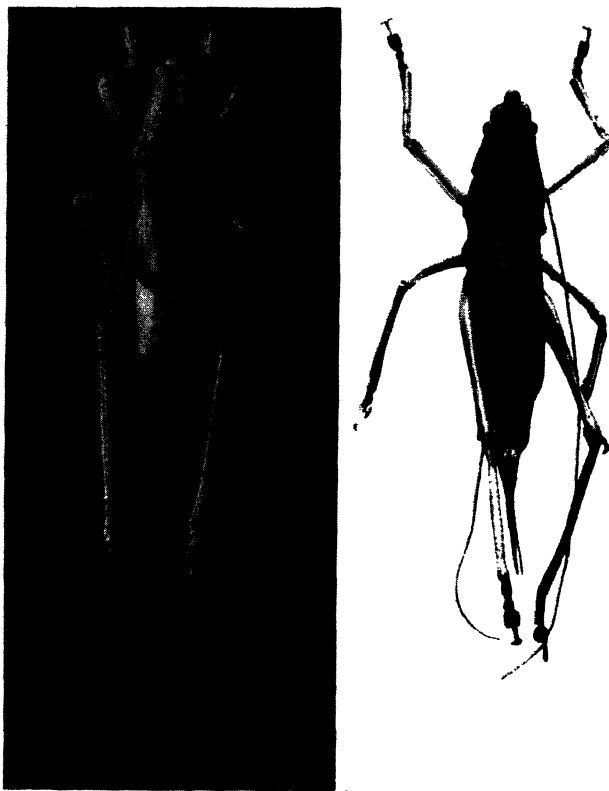


Figure 71—*Banza nitida* (Brunner). Male, left; female, right. (Not to same scale.)

***Banza parvula* (Walker) (fig. 72).**

Saga parvula Walker, 1869:293. Genotype of *Banza*.

Banza nigrifrons Walker, 1870:477.

Microsaga parvula (Walker) Saussure, 1888:155. Genotype of *Microsaga*.

Conocephalus blackburni Bormans, 1882:346, 3 figs.

Brachymetopa blackburni (Bormans) Redtenbacher, 1891:431.

Brachymetopa discolor Redtenbacher, 1891:431, fig. 49. Genotype of *Brachymetopa*.

Perkins, 1899:9, pl. 1, figs. 1, 1a; pl. 2, figs. 1, 1a. 1910:687. 1913, pl. 15, figs. 1-4.

Endemic. Oahu (type locality of all five names).

Parasite: *Eupelmus axestops* Perkins (Hymenoptera: Eupelmidae) in the eggs.

Eggs cigar-shaped, 6-7 mm. long.

This species has erroneously been reported from Formosa and the Ryukyu Islands.



Figure 72—*Banza parvula* (Walker), male (top) and female.

Banza unica (Perkins) (fig. 69).

Brachymetopa unica Perkins, 1899:10.

Hebard, 1922:344.

Endemic. Oahu (type locality: mountains near Honolulu).

Subfamily CONOCEPHALINAE

Genus **CONOCEPHALUS** Thunberg, 1815

Conocephalus saltator (Saussure) (fig. 73).

Xiphidium saltator Saussure, 1859:208.

Xiphidium varipenne Swezey, 1905:216, pl. 14.

Called *Xiphidium fuscum* Fabricius by error of identification in Hawaiian literature prior to 1905.

Oahu, Molokai, Hawaii, Midway.

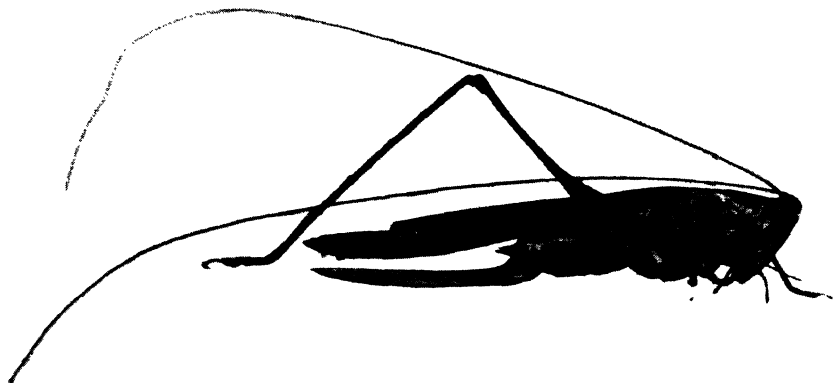


Figure 73—*Conocephalus saltator* (Saussure), female.

Immigrant. Widespread in tropical America. First recorded from Hawaii by Brunner in 1895.

Hosts: *Pseudococcus brevipes*, sugarcane bud moth (*Ercunetis flavistriata* Walsingham) and other caterpillars, dipterous larvae, sugarcane leafhopper (*Perkinsiella saccharicida* Kirkaldy).

Hostplants: blossoms of morning glories, *Canna*, lantana; leaves of young sugarcane, corn, honohono grass, rice, potato, bean blossoms, coffee; rice pollen; ripe guava fruits; occasionally damages pineapples by laying eggs in flowers of young fruit. On occasion this species has caused damage to corn and rice "in the milk," by biting into the heads and eating out the succulent young grain.

Parasites: *Isodontia harrisi* Fernald (Hymenoptera: Sphecidae) on nymphs and adults; *Centrodora xiphidii* (Perkins) (Hymenoptera: Eulophidae) and *Brachistella lutea* (Fullaway) (Hymenoptera: Trichogrammatidae) on eggs.

The stridulation of this species is a rapid chirring which reminds me of the sound of a small electric motor whose brushes squeak as it turns.

Bionomical and morphological studies by Swezey, 1905:212–223. Two to 15 eggs inserted in a group in plant tissue; incubation period from 2 to 5 weeks; 6 molts at 6- to 23-day instars; egg to adult-hood in $2\frac{1}{2}$ to $3\frac{1}{2}$ months; tegmina and wings extremely variable in length, brachypterous or fully developed for flight.

Subfamily LISTROSCELINAE

Genus **XIPHIDIOPSIS** Redtenbacher, 1891

Xiphidiopsis lita Hebard (figs. 74, 75).

Xiphidiopsis lita Hebard, 1922:345. Swezey, 1929:279.

Kauai, Oahu, Maui, Hawaii (type locality: Hilo).

Immigrant. First found by Pemberton at Hilo, Hawaii, in 1919; first found on

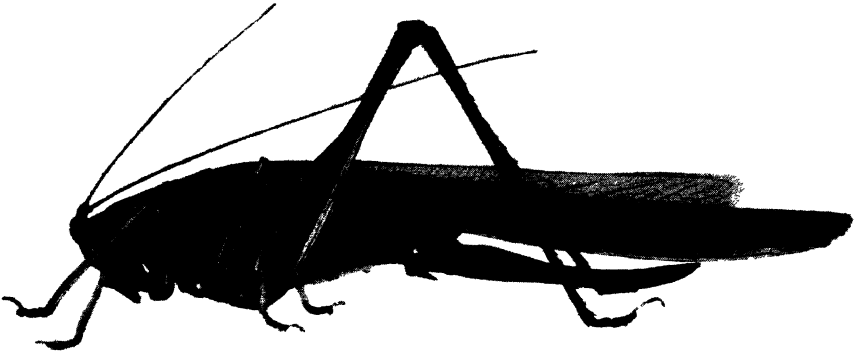


Figure 74—*Xiphidiopsis lita* Hebard, paratype female. No males of this longhorned grasshopper have ever been found. The females reproduce without fertilization.

Oahu at Honolulu by Fullaway, 1923. Origin unknown for many years, but now known from the Society and Marquesas Islands and probably widely distributed in Polynesia.

Hosts: aphids, lepidopterous larvae.

Hostplants: reported occasionally to eat some flower blossoms.

Parthenogenetic; no males known either in Hawaii or elsewhere.

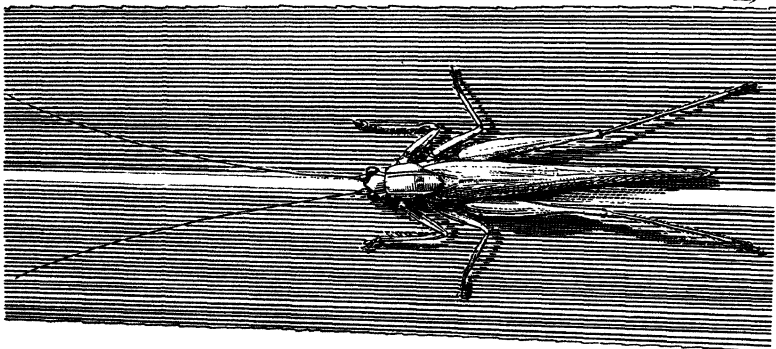


Figure 75—*Xiphidiopsis lita* Hebard, resting in a characteristic position on a sugarcane leaf. (From Williams' original drawing, 1931.)

Family GRYLLIDAE Saussure, 1894

Crickets

Leaping insects; head exposed, prominent in most species, prognathus in some genera; face vertical or almost so in most groups; antennae variable, but longer than body in most species (shorter than head and prothorax only in *Gryllotalpa*), setaceous, many-segmented, inserted between eyes or between and below eyes;

compound eyes not very large, but conspicuous; ocelli present or absent; mandibles large, prominent, dentate; maxillary palpi five-segmented; labial palpi three-segmented; pronotum large, shield-like or saddle-like; wings variable, present or absent, fully developed or brachypterous; tegmina, when fully developed, longitudinally angulate and bent downward along sides of body and flat dorsally, modified into strongly developed stridulating organs in males; abdomen 10-segmented; with nine complete tergites visible; males with nine complete ventrites, females with seven; ovipositor variable, wanting in *Gryllotalpa*, but exerted, long and well-developed in most forms, composed of four slender sclerites; cerci elongate, not segmented; hind legs with femora and tibiae strongly developed for leaping (excepting *Gryllotalpa*); fore tibiae bearing the tympanal organs when they are present; tarsi three-segmented, first segment elongate, second shortened, pulvilli absent in most species; tarsal claws divaricate or divergent, without empodia; oviparous, eggs deposited in soil, either singly or in groups, or in plant tissues; nocturnal insects of herbivorous or omnivorous habit.

There have been 42 crickets recorded from Hawaii. The family reaches its greatest diversity in the tropics; and there are over 1,000 species described from the world. There are both immigrant and endemic species in the Hawaiian fauna. In the endemic section there have been 33 species described in six genera, five of which are endemic. The eight immigrant species are included in six genera. The group is the most diversified family of the Hawaiian Orthoptera. The smallest members of the order belong here (*Myrmecophila*).

The crickets are the best known of insect songsters and are rivaled, but not equaled, only by the katydids. In some places in the world crickets are kept in cages so that their captors may enjoy their songs and chirpings. Stridulation is accomplished by the male which raises his tegmina at an angle above the abdomen and rubs them across one another. A file-like area on one tegmen rubs across a specialized, sclerotized area on the other tegmen, thus vibrating a drum-like membrane and causing the characteristic sound. Unlike most Orthoptera, the right tegmen of the male crickets normally overlaps the left, instead of vice versa. The chirping of some of our endemic forest crickets has been accredited to arboreal Mollusca, which the Hawaiians thought were singing land snails.

Crickets may be found in Hawaii from burrows in the soil to tree tops, from seashore to mountain top; the members of one genus are myrmecophiles.

KEY TO THE CRICKET SUBFAMILIES FOUND IN HAWAII

1. Fore legs expanded, greatly modified for burrowing, their tibiae and first tarsal segments armed with great, blade-like teeth **Gryllotalpinae.**
- Fore legs slender, not fitted for burrowing..... 2
- 2(1). Tarsi with the second segment laterally compressed, usually small, obscure and more or less hidden in apex of tibia.... 3

- Tarsi with the second segment exposed and distinct, dorso-ventrally depressed in most species (laterally compressed in some endemic Eneopterinae, but then fully exposed and conspicuous) 5
- 3(2). Small, apterous, myrmecophilous crickets not more than 5 mm. long; head partly retracted into prothorax; eyes small, partly covered by pronotum; hind femora abnormally broad and expanded, ovate, less than twice as long as broad **Myrmecophilinae.**
- Larger insects; head not retracted, eyes fully exposed and separated from pronotum; hind femora elongate, more than twice as long as broad..... 4
- 4(3). Body squamose; hind tibiae with some apical spines and spurs and at most a row of small tooth-like or seta-like spines along each dorsal margin, but without large dorsal spines above apex part of **Mogoplistinae.**
- Body not squamose; dorsa of hind tibiae armed on each side with a row of numerous large, strong, long, conspicuous spurs **Gryllinae.**
- 5(2). Hind tibiae with about six long, dorsal, dactyl-like spurs above apex and without teeth-like spines; ovipositor blade-like, strongly compressed, conspicuously arcuate, scimitar-like **Trigonidiinae.**
- Hind tibiae with a row of many short, tooth-like dorsal spines along each margin, but without any long spurs above apical group; ovipositor subcylindrical, almost straight or gently arcuate, but not scimitar-like..... 6
- 6(5). Body conspicuously squamose; hind tibiae somewhat more than one-half as long as femora, but not almost as long part of **Mogoplistinae.**
- Body not squamose; hind tibiae as long or about as long as hind femora **Eneopterinae.**

Subfamily GRYLLOTALPINAE

Genus **GRYLLOTALPA** Latreille, 1802

Gryllotalpa africana Palisot de Beauvois (fig. 76).

Gryllotalpa africana Palisot de Beauvois, 1805:229, pl. Orthoptera IIc, fig. 6.
Williams, 1931:70, pl. 6. Tindale, 1928:11-16, fig. 4.

The African mole cricket.

Kauai, Oahu, Maui.

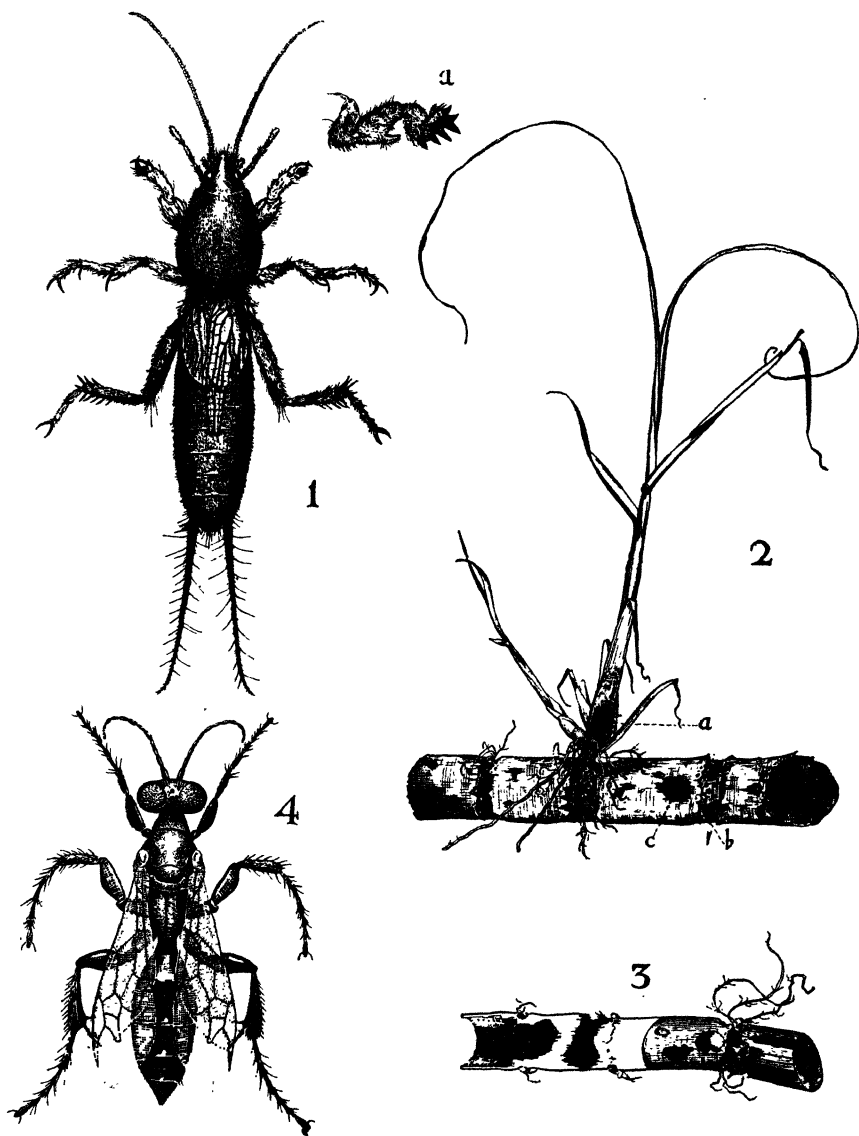


Figure 76—*Gryllotalpa africana* Palisot de Beauvois. 1, Adult; 1a, fore leg to show the modifications for digging. 2, A piece of injured "plant cane," showing at a, a young shoot which has been eaten into and killed and a new shoot starting out at the left; b, a destroyed "eye," and a hole eaten through the rind at c. 3, A much-eaten piece of cane partially sectioned to show internal injury. 4, *Larva lusoensis* Rohwer, a Philippine wasp introduced to prey on the cricket. (After Swezey, 1923.)

Immigrant. Widespread. Africa, China, Philippines, Formosa, Japan, Java, Australia, New Zealand. Recorded by Koebele as common on Oahu in 1896 (1896:594).

Hosts: earthworms, scarab larvae (*Adoretus*, *Aphodius*).

Parasite: *Larra luzonensis* Rohwer (Hymenoptera: Larridae), on nymphs and adults.

Predator: mongoose.

The mole cricket may burrow down three or four feet in the soil. Its burrows cause leaks in irrigation canal walls and taro-field dikes; it eats the eyes and young shoots of seed sugarcane in some low-lying, damp or swampy sugarcane fields, and it has caused up to 75 percent killing of seed cane in some localities in past years. However, little damage is now reported in sugarcane fields. "The eggs are laid in a group in a specially prepared brood chamber and the young require some months to become full grown" (Williams, 1931:71). Tindale (1928) gives a good account of the species.

Wisecup (1943), working on the mole crickets of the southeastern United States (different species from ours), where an estimated injury of two million dollars is caused annually, says that "Mole crickets damage crops by feeding on the roots, root stems, tubers, or fruits of the plants and also by burrowing in the upper inch or two of the soil about the roots, causing affected plants to dry out or uprooting them. Sprouting seedlings or transplants of many crops are specially subject to injury through being fed upon or uprooted. Since one mole cricket in burrowing can cover several yards of territory in a single night, the damage done by only a few specimens per square yard sometimes completely destroys a seed bed in a few nights." He has found the following poisoned bait effective: 100 pounds of dry wheat bran and 8 pounds sodium fluosilicate moistened with 3 to 5 gallons of water and thoroughly mixed. This is strewn evenly over infested fields at about 20 pounds of dry mixture per acre and repeated once or twice at 10-day intervals.

Subfamily GRYLLINAE

KEY TO THE GENERA FOUND IN HAWAII

1. Tegmina short, leaving about one-half or more than one-half of abdomen exposed; narrowest part of interantennal area of face hardly if any broader than greatest transverse chord of an antennal fossa **Gryllobates** Saussure.
2. Tegmina elongate, concealing almost all of abdomen; narrowest part of interantennal area of face obviously broader than greatest transverse chord of an antennal fossa, about one and one-half or up to twice as broad..... **Acheta** (Linnaeus).

Genus **GRYLLODES** Saussure, 1874

Grylloides sigillatus (Walker) (fig. 77).

Gryllus sigillatus Walker, 1869:46.

Gryllus pustulipes Walker, 1869:51.

Gryllus poeyi Saussure, 1874:420, pl. 7, fig. 8.

Kauai, Oahu, Molokai, Maui, Kahoolawe, Hawaii.

Immigrant. Mauritius, India, Australia, North, Central and South America.
First recorded from Hawaii by Brunner in 1895.

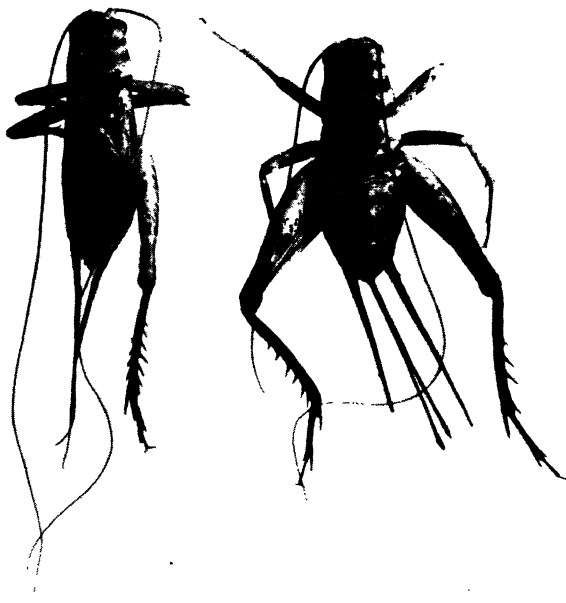


Figure 77—*Grylloides sigillatus* (Walker). Male, left; female, right.

Genus **ACHETA** (Linnaeus)

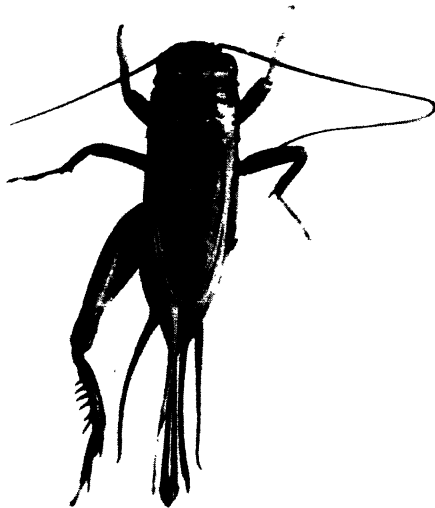
Gryllus (*Acheta*) Linnaeus, 1758:428.

Gryllulus Uvarov, 1935:320.

For discussion of synonymy, see Roberts, 1941:33-34.

KEY TO THE SPECIES FOUND IN HAWAII

1. Length of body excluding terminalia 15–20 mm. or more; head normally without a distinct pale fascia between posterior ocelli, but if a narrow pale line is present it is broadly Λ -shaped; crown with several rather obscure pale vittae, but not tending to coalesce so as to make entire base of head appear pale; shortest distance between inner margins of antennal fossae twice as broad as first antennal segment.....*oceanica* (LeGuillou).
2. Length of body excluding terminalia less than 15 mm.; head with a conspicuous, slightly arcuate, moderately broad, pale fascia extending from eye to eye across posterior ocelli; crown usually predominantly pale, tending to have a broad, pale band entirely around base of head, this area usually with short pale vittae; shortest distance between inner margins of antennal fossae distinctly less than twice as broad as first antennal segment.....*conspersa* (Schaum).

Figure 78—*Acheta conspersa* (Schaum), female.

***Acheta conspersa* (Schaum) (fig. 78).**

Gryllus conspersus Schaum, 1862:117.

Kauai, Oahu, Hawaii.

Immigrant. Africa, India, Japan, Formosa, Ryukyu Islands, Indo-Pacific. Collected by Perkins, but not recorded by name until Hebard listed it in 1922 (p. 350).

***Acheta oceanica* (LeGuillou) (fig. 79).**

Gryllus oceanicus LeGuillou, 1841:293.

Gryllus innotabilis Walker, 1869:47.

Lyon, 1914:180, figs. 2, 3, adult and injury to pineapple. Swezey, 1918:9, figure showing damage to sugarcane.

The oceanic field cricket.

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii.

Immigrant. Widespread in Oceania from the Malay Peninsula eastward, including Penang, Borneo, New Hebrides, Solomons, Fiji, Samoa, Tonga, Society Islands, Marquesas (type locality: Nukuhiva), Easter Island; also recorded from Japan. It was widespread in the Hawaiian Islands when first recorded by Bormans in 1882.

Food: It eats most any vegetable matter available. It is recorded to eat occasionally into pineapple fruits, damaging the fruit and allowing entrance of fungi and bacteria and to gnaw the leaves; also damages sugarcane by eating holes in canes in contact with ground litter. Swezey (1918) reported 10 percent of such prostrate canes damaged in some localities. For control, Lyon (1914) suggested using poison baits made with molasses; such baits are readily eaten by the crickets.

Parasite: *Notogonidea subtessellata* (F. Smith) (Hymenoptera: Larridae), on nymphs and adults.

Predator: The mongoose eats quantities of these crickets.



Figure 79—*Acheta oceanica* (LeGuillou), the oceanic field cricket. Male, left; female, right.

Bionomical studies by Swezey (1918:9). Eggs deposited singly in soil, 2.3×0.5 mm., whitish; incubation period about three weeks; nymphal stage between four and five months; adults live two months or more. The steady rhythmic beat of this field cricket is commonly heard on warm summer nights. I have seen the males stand with their legs widely spread and their tegmina uplifted a bit and rapidly vibrating as they chirp. Now and again two males will fight a speedy, lusty battle and then each retire to continue his throbbing chirping.

Subfamily MYRMECOPHILINAE

Genus MYRMECOPHILA Latreille, 1829

Myrmecophilus Berthold, 1827.

These tiny crickets live in ants' nests.

KEY TO THE SPECIES FOUND IN HAWAII

1. Mesonotum obviously paler than pronotum; dorsal, inner margin of hind tibia with three spines above apical spurs, each progressively longer, counted toward apex of tibia; outer dorsal margin with a single spine similar to second spine in inner row but situated well distad of it. **americana** Saussure.
2. Mesonotum concolorous with pronotum; dorsal inner margin of hind tibia with four spines above the long apical spurs, alternating in length, a short, a long, a short and a long spine counted toward apex of tibia; outer dorsal margin with a single spine above apical spur about as long as second spine in inner row and situated slightly distad of it. **quadrispina** Perkins.



Figure 80—*Myrmecophila quadrispina* Perkins. A tiny cricket which lives in ant nests

Myrmecophila americana Saussure.

Myrmecophila americana Saussure, 1877:461.

Oahu.

Immigrant. South America, India. First recorded in Hawaii by Hebard (1925:302) from specimens collected in 1924.

Host ant: *Paratrechina longicornis* (Latreille).

Myrmecophila quadrispina Perkins (fig. 80).

Myrmecophila quadrispina Perkins, 1899:14, pl. 2, fig. 7. Hebard, 1922:351, expanded redescription.

Kauai, Oahu (type locality: Honolulu).

Immigrant. Described from Hawaii, but now known from Samoa and also recorded from Hongkong. Perkins (1913:ccxvii) mentions intercepting it from shipments of plants in quarantine at Honolulu. Hebard (1933:65) considers that the extra-Hawaiian records need verification.

Host ants: *Pheidole megacephala* (Fabricius), *Solenopsis geminata rufa* (Jerdon), *Paratrechina* species.

Subfamily MOGOPLISTINAE

KEY TO THE GENERA AND SPECIES FOUND IN HAWAII

1. Length greater than 10 mm.; when viewed from side, the strongly protuberant front of head is obviously discontinuous in longitudinal outline with top of head; hind tibiae with a well-defined row of conspicuous, dark-tipped teeth along each dorsal margin; first hind tarsal segment about one-third as long as a hind tibia, with a row of conspicuous, dark-tipped teeth along each dorsal margin; second tarsal segment conspicuous **Cycloptilum bimaculatum** (Shiraki).
2. Length less than 8 mm.; front of head forming an almost continuous longitudinal outline with top of head; hind tibiae without dorsal marginal teeth, but with slender, inconspicuous, seta-like spines only; first hind tarsal segment more than one-half as long as a hind tibia, with dorsal seta-like spines but no teeth; second tarsal segment inconspicuous. **Cycloptiloides americanus** (Saussure).

Genus **CYCLOPTILUM** Scudder, 1868

Liphoplus Saussure, 1876:77.

Cycloptilum bimaculatum (Shiraki) (fig. 81).

Liphoplus bimaculatus Shiraki, *Insecta Matsumurana* 4:192, fig. 5, 1930.

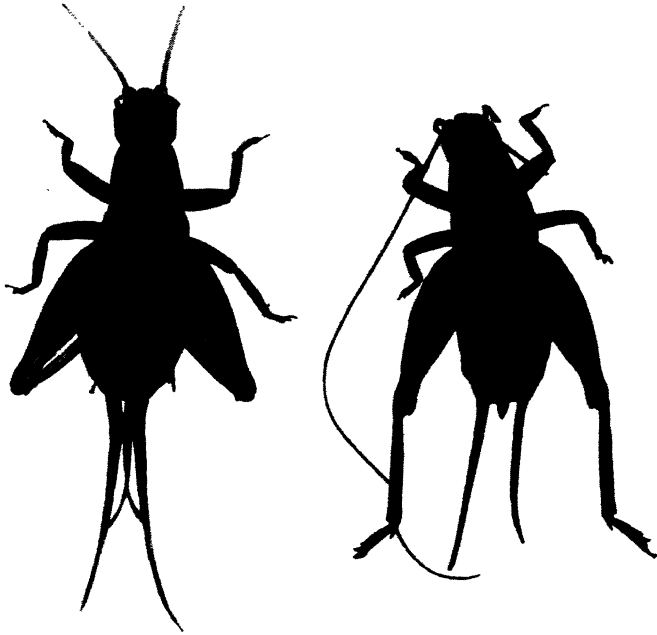


Figure 81—*Cycloptilum bimaculatum* (Shiraki). Male, right; female, left.

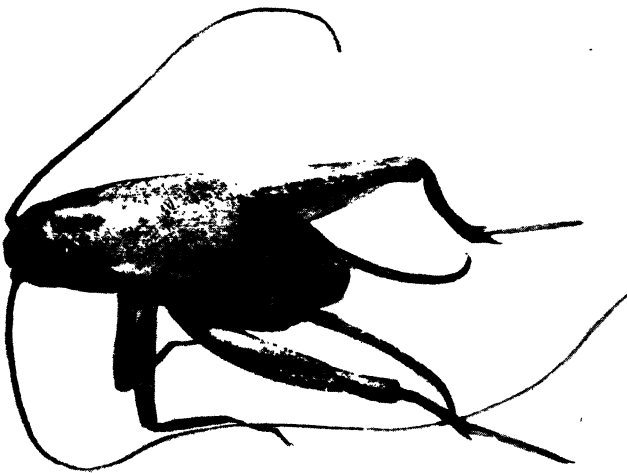


Figure 82—*Cycloptiloides americanus* (Saussure).

Kauai, Oahu.

Immigrant. Described from Formosa. First recorded by Pemberton in 1940 (1941) from specimens found in a house in Honolulu.

Genus **CYCLOPTILOIDES** Sjöstedt, 1909

Glaphyropus Rehn and Hebard, 1912.

Cycloptiloides americanus (Saussure) (fig. 82).

Cycloptilum americanus Saussure, 1874:426, pl. 8, figs. 41, 42.

Misnamed *Paranemobdus schauinslandi* Alfken in early Hawaiian literature.

Kauai, Oahu, Molokai, Hawaii.

Immigrant. First recorded by Perkins from Honolulu (1910:688). Central America.

Habit: in rubbish; in houses, where it is most often found in sinks, bathrooms, or other places where water or moist conditions are available. It becomes more abundant in damp weather. Stridulation is accomplished by an up-and-down movement of the prothorax.

Subfamily **TRIGONIDIINAE**

KEY TO THE GENERA OF TRIGONIDIINAE FOUND IN HAWAII

1. Wings fully developed for flight, much longer than abdomen part of **Metioche** Stål.
 Wings not developed for flight, at most only slightly surpassing abdomen 2
2. Venation of both tegmina of male essentially similar; tegmina of female with only about four complete longitudinal, dorsal veins between the vein at top of lateral declivitous part and inner edge, and these not connected by numerous cross-veins part of **Metioche** Stål.
 Venation of tegmina of male conspicuously different, right tegmen broad and flat above, with a well-developed transverse "vena-stridulans" and complete "mirror" at base; tegmina of female with more than four veins, usually about seven, veins close together and connected by many cross-veins or pseudo-cross-veins from base to apex.....**Paratrigonidium** Brunner.

Genus **PARATRIGONIDIUM** Brunner, 1893

This genus constitutes the second complex of endemic species of Hawaiian Orthoptera, and, together with the species of *Banza* and the Prognathogryllini which follow, it makes up a characteristic element in the native insect fauna of Hawaii. *Paratrigonidium* was described from Burma and Java and now is known also from the Philippines, Formosa and Japan. It closely resembles such allied extra-Hawaiian genera as *Metioche* and *Anaxipha*, which are found widespread in the islands to the south and southwest. Dr. Chopard tells me that he feels that

our species are "very different from the type species" of the genus. The matter needs careful study. The Trigonidiinae is a systematically difficult assemblage.

All our species are flightless. The wings and tegmina develop equally well up to the last molt, but at that ecdysis the hind wings are lost. However, the loss of the powers of flight is partially counteracted by the extraordinarily developed powers of leaping. Some of the species can jump several feet at a time and are most difficult to capture.

One of our species (*P. pacificum*) is largely terrestrial, but the remainder of the forms are mostly arboreal in habit and are to be found on ferns, shrubs and trees. Some species appear to be host-specific and are confined to one kind of fern, shrub or tree. In fact, one species (*P. atroferrugineum*) is said by Perkins to be so host-specific as to be attached to only one variety of the multiform tree *Metrosideros polymorpha*. Several species hide beneath the bark of trees. Most of the species are nocturnal, but some are to be found active during the day in the gloom of canyons and forest. Some species chirp during the day as well as being more active at night. Perkins (1899:15) said, "There is a considerable difference between the songs of some of the species, and in some cases the sound can be heard at a great distance." It is the chirping of these crickets that gave rise to the Hawaiian myth of the singing land snails.

The young of the foliage-frequenting species are generally green, whereas those of the terrestrial or bark-frequenting species are brownish.

These crickets are much sought by some of the endemic Hawaiian birds. Perkins records one drepaniid (*Viridonia sagittirostris*) as feeding extensively on the Freycinetia-frequenting *Paratrigonidium freycinetiae*.

I have no record of any insect parasites of the group, but Perkins (1913:ccxviii) and Hebard (1922:358) record *Gordius* roundworm parasites, and I have also seen them. I have seen the native nabid bug, *Nabis lusciosus* White, feeding on the nymphs of the terrestrial *P. pacificum* Scudder on Oahu.

A note sent by Dr. Perkins with a box of specimens of *Paratrigonidium* states that "The whole second set—the first of course went to the British Mus.—was given to Brunner V.W., on account of the help given at the start. I myself did not have any of the collection described in F. H. [*Fauna Hawaiiensis*] except the left over specimens of the huge series of *P. pacificum*."

It is unfortunate that the beauty of these crickets is mostly lost after death. A collection of them becomes a rather drab lot because of fading or darkening of their colors, but in life many are distinctly colored and are attractive insects. Degreasing by soaking in ether will make specimens more attractive and will aid in making certain markings more evident.

The species are not well-known, and I feel that there is a certain amount of confusion regarding them. The preparation of a key to the species is not an easy task, and I am far from satisfied with the present attempt. Certain of the species have been represented by only one or a few specimens in the collections available for study. I have not seen *robustum* from Kauai and it is not included in the following key.

KEY TO THE HAWAIIAN PARATRIGONIDIUM

(Excepting *robustum*)

1. Lateral field (declivitous part) of male tegmina with eight veins basad, as in figure 83; male subgenital plate elongate, subconical, concealing the genital valves which do not bear long arms from their external sides; ovipositor with the "transverse suture" nearer base than apex (measured along dorsal edge); a terrestrial species on all main islands *pacificum* Scudder.
- Not such species, the lateral tegminal field of male usually with only six veins, rarely with seven; male subgenital plate, even if shaped somewhat as above, not concealing the long processes ("claspers") of the genital valves; ovipositor with the "transverse suture" nearer apex than base 2



Figure 83—Sketches of lateral tegminal fields of males of *Paratrigonidium attenuatum* Perkins, left, and *P. pacificum* Scudder, right, to show differences in venation. The venation is variable within these species.

- 2(1). Kauai species 3
Not so 5
- 3(2). A comparatively pale species, predominantly testaceous; subgenital plate (terminal ventrite) of male deeply concavely emarginate at apex; speculum of male tegmen "very narrow" *attenuatum* Perkins.
Brownish, not predominantly testaceous species; apex of subgenital plate of male not deeply concave 4
- 4(3). Male subgenital plate with a distinct, although small, median, caudal protuberance *crepitans* Perkins.
Male subgenital plate nearly evenly, broadly, shallowly concave behind, the median part of hind margin not produced into a process *varians* Perkins.
- 5(2). Oahu species 6
Not so 10
- 6(5). An almost entirely pale species (excepting male abdomen) tinged with pink or reddish (largely lost after drying), legs nearly or quite immaculate; tegmina of male without a dark macula behind vena stridulans; male subgenital plate nearly subtruncate apically with the middle slightly produced *subroseum* Perkins.
Without such a combination of characters 7
- 7(6). Right male tegmen without a dark macula behind vena stridulans; genital "claspers" with teeth reduced, the subapical one obsolete, the terminal one minute 8

- Right male tegmen with area behind vena stridulans dark;
genital "claspers" each with two well-developed teeth,
although the subapical one may be slender..... 9
- 8(7). Fore and mid femora entirely dark, hind femora dark
along dorsal edges and contrasting with paler color of
head, pronotum and tegmina; subgenital plate deeply
concave behind; cerci more than 3 mm. long.....
.....**saltator** Perkins.
Femora not contrasting in color with head, pronotum and
tegmina; subgenital plate produced at middle; cerci only
about 2.5 mm. long**exiguum** Perkins.
- 9(7). Subgenital plate of male produced at middle of hind
margin**debile** Perkins.
Subgenital plate of male nearly evenly, broadly, shallowly
concave behind, not produced at middle....**varians** Perkins.
- 10(5). Molokai species 11
Not so 13
- 11(10). Femora black with red apices; tibiae reddish; male teg-
mina with entire disk dark with edges and lateral fields
orange and reddish; a striking species.....
.....**atroferrugineum** Brunner.
Not such species; predominantly brown, maculate.....12
- 12(11). Head between antennae black; clypeus black.....
.....**molokaiense** Perkins.
Head and clypeus brown and testaceous, maculate.....
.....**varians** Perkins.
- 13(10). Maui species 14
Not so 15
- 14(13). Head, base of antennae, femora and hind tibiae reddish
or pinkish**roseum** Perkins.
Brownish and testaceous species.....**varians** Perkins.
- 15(13). Lanai species**varians** Perkins.
Hawaii species 16
- 16(15). Right male tegmen with a number of dark marks similar
in color to the dark color in the vena stridulans area but
scattered over all; dark marks on legs outstanding, tibiae
conspicuously annulate; pale greenish in life.....
.....**viridescens** Perkins.
Not such species, dark color on right male tegmen confined
to neighborhood of vena stridulans or entire tegmen
infusate 17
- 17(16). Largest species in Hawaii, about 8.5 to 9.5 mm. in length
from front of head to apex of tegmina; tegmina more
than 5 mm. long.....**grande** Perkins.
Smaller species, less than 7.5 mm. in length, with tegmina
not over 5 mm. long.....18
- 18(17). Fore and mid femora entirely dark and contrasting with
the pale, annulate tibiae.....**freycinetiae** Perkins.
Fore and mid femora not dark colored.....19

- 19(18). Legs indistinctly maculate, if at all spotted; hind tibiae
 almost entirely pale**filicum** Perkins.
 Legs distinctly maculate and/or annulate; hind tibiae
 mostly dark**varians** Perkins.

Paratrigonidium atroferrugineum Brunner.

Paratrigonidium atroferrugineum Brunner, 1895:895. Perkins, 1899:17, pl. 1, fig. 10.

Endemic. Molokai (type locality: 4,000 feet).

Hostplant: *Metrosideros*.

Hebard (1922:360) stated that "This, the handsomest known species of the genus, ranks among the most distinctively and beautifully colored Gryllidae of Earth."

The nymphs are green.

Paratrigonidium attenuatum Perkins (figs. 83, 84).

Paratrigonidium attenuatum Perkins, 1899:20, pl. 1, fig. 13; pl. 2, fig. 5.

Paratrigonidium attenuatum variety *major* Perkins, 1899:20, new synonym.

Paratrigonidium attenuatum variety *minor* Perkins, 1899:20, pl. 2, fig. 5, new synonym.

Endemic. Kauai (type locality: 4,000 feet).

Habit: under bark of large trees.

No mention of this species was made either by Kirby (1906) or Hebard (1922).

Paratrigonidium crepitans Perkins.

Paratrigonidium crepitans Perkins, 1899:19. Hebard, 1922:359.

Endemic. Kauai (type locality: 4,000 feet).

Habit: in piles of dead wood and in low shrubbery.

Paratrigonidium debile Perkins.

Paratrigonidium debile Perkins, 1899:21. Hebard, 1922:356.

Endemic. Oahu (type locality: mountains above 2,000 feet).

Paratrigonidium exiguum Perkins.

Paratrigonidium exiguum Perkins, 1899:21.

Endemic. Oahu (type locality: Waianae Mountains, 3,000 feet).

Habit: arboreal.

Paratrigonidium filicum Perkins.

Paratrigonidium filicum Perkins, 1899:17, pl. 2, fig. 6. Hebard, 1922:356, pl. 27, fig. 2.

Endemic. Hawaii (type locality: Oloa, 2,000 feet).

Hostplant: a "tall fern."

The nymphs are green.

Paratrigonidium freycinetiae Perkins (fig. 84).

Paratrigonidium freycinetiae Perkins, 1899:16.

Endemic. Hawaii (type locality: Oloa, 2,000 feet).

Hostplant: *Freycinetia*.

Predator: the drepaniid bird *Viridonia sagittirostris*.

Paratrigonidium grande Perkins (fig. 84).

Paratrigonidium grande Perkins, 1899:19, pl. 1, fig. 12. Hebard, 1922:355, pl. 27, fig. 1.

Paratrigonidium "gracile" Perkins, Hebard, 1926:301 (name cited in error).

Endemic. Hawaii (type series from Puna, Kau and Kona).

Habit: under bark of trees.

The nymphs are brownish.

Paratrigonidium molokaiense Perkins (fig. 84).

Paratrigonidium molokaiense Perkins, 1899:20.

Endemic. Molokai (type locality: 3,000 feet).

Habit: frequents low shrubbery.

Paratrigonidium pacificum Scudder (figs. 83, 84).

Paratrigonidium pacificum Scudder, 1868:139. Brunner, 1895:895. Perkins, 1899:22, pl. 2, fig. 6a. Hebard, 1922:361, pl. 27, fig. 6.

Endemic. Kauai, Oahu, Molokai, Lanai, Maui, Hawaii (type locality: "Hawaiian Islands," unique female; the first described Hawaiian species).

Predator: *Nabis lusciosus* White (Heteroptera: Nabidae).

Habit: more terrestrial than the other species.

This is a common ground form, and the forest rings with its chirping wherever it is found. It may be collected in large numbers if a paper or similar article is laid out on a trail or over the grass in its habitat, for the crickets will congregate beneath it. A partially opened paper sack will lure them inside where they can be easily secured.

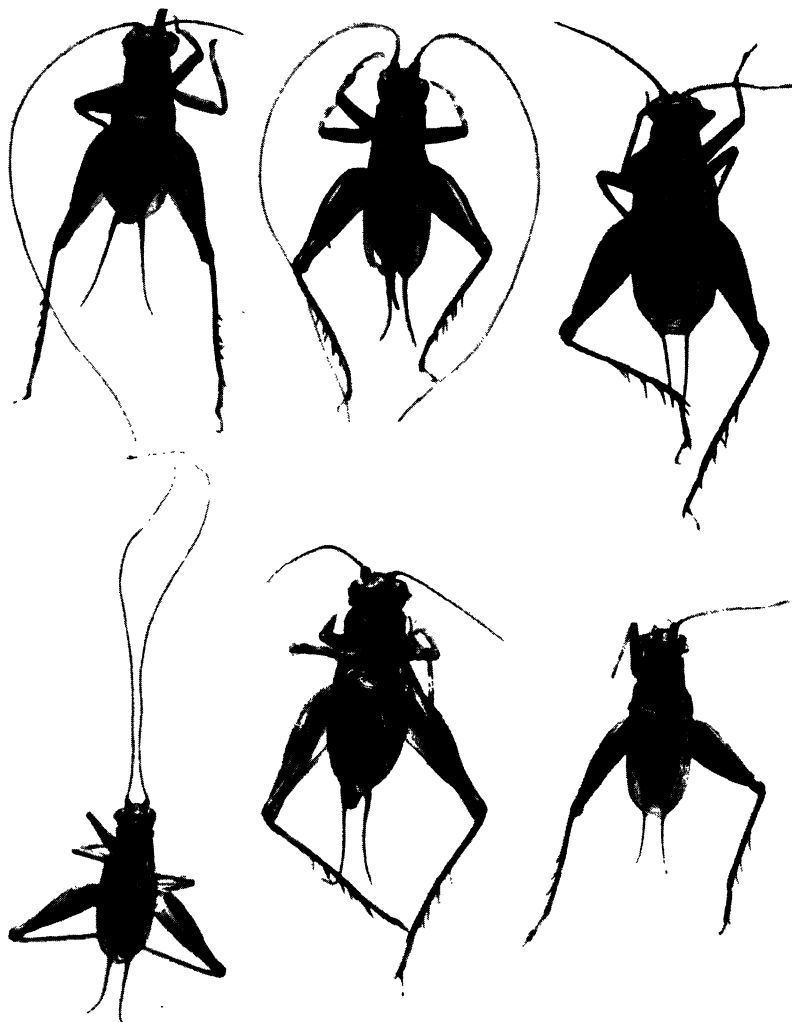


Figure 84—*Paratrigonidium* species. Top row, left to right: *P. attenuatum* Perkins; *P. freycinetiae* Perkins (female, all the others are males); *P. grande* Perkins. Bottom row, left to right: *P. molokaiense* Perkins; *P. pacificum* Perkins; *P. subroseum* Perkins. Old specimens such as these make poor subjects for photography.

***Paratrigonidium robustum* Perkins.**

Paratrigonidium robustum Perkins, 1899:20.

Endemic. Kauai (type locality: 4,000 feet, unique male).

Habit: under bark of trees.

I have not seen this species.

Paratrigonidium roseum Perkins.

Paratrigonidium roseum Perkins, 1899:16, pl. 1, fig. 9. Hebard, 1922:355, fig. 1.

Endemic. Maui (type locality: West Maui, 3,000 feet, unique female).

Hostplant: *Metrosideros*.

Paratrigonidium saltator Perkins.

Paratrigonidium saltator Perkins, 1899:16. Hebard, 1922:359.

Endemic. Oahu (type locality: above 2,000 feet).

Hostplant: *Freycinetia*.

Paratrigonidium subroseum Perkins (fig. 84).

Paratrigonidium subroseum Perkins, 1899:17. Hebard, 1922:352.

Endemic. Oahu (type locality: 2,000 feet).

Hostplant: *Metrosideros*.

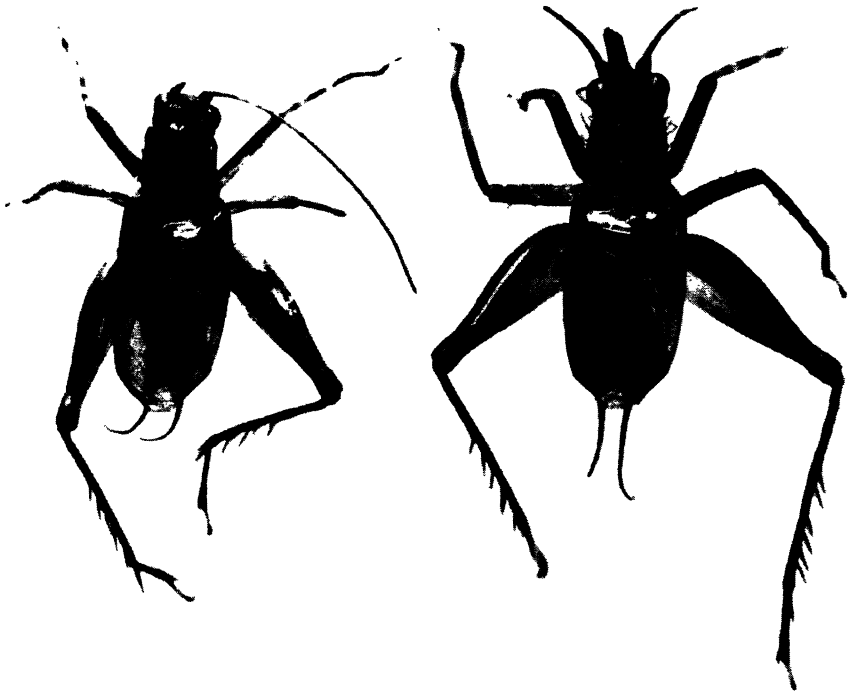


Figure 85—*Paratrigonidium viridescens* Perkins, male, left; *P. varians* Perkins, male, right.

Paratrigonidium varians Perkins (fig. 85).

Paratrigonidium varians Perkins, 1899:18. Hebard, 1922:357, pl. 27, figs. 3, 4.

Endemic. Kauai, Oahu, Molokai, Maui, Lanai, Hawaii (type series from Kauai, Oahu, West Maui, and Hawaii).

Habit: arboreal.

Paratrigonidium viridescens Perkins (fig. 85).

Paratrigonidium viridescens Perkins, 1899:18, pl. 1, fig. 11.

Endemic. Hawaii (type locality: Olaa, 2,000 feet).

Hostplant: "Lives amongst a beautiful creeping fern [*Lindsaya macraeana* ? E.C.Z.], which clothes the tree trunks in wet forests" (Perkins, 1899).

Genus METIOCHE Stål, 1877

This genus is widespread in the south and western tropical Pacific and Malaya. One species has recently gained entrance to Hawaii.

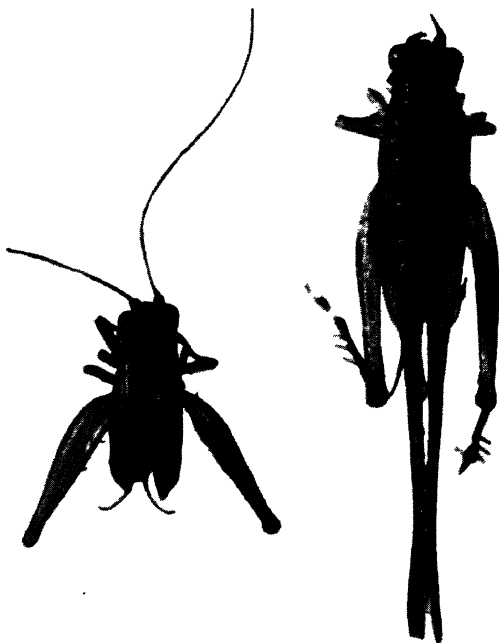


Figure 86—*Metioche vittaticollis* (Stål), brachypterous male, left; long-winged female, right.

***Metioche vittaticollis* (Stål) (fig. 86).**

Trigonidium vittaticollis Stål, 1860:317.

Kauai, Oahu.

Immigrant. First collected in Hawaii by F. X. Williams late in 1944 among grasses and low herbage in his yard at Makiki, Honolulu. A widespread Pacific species.

Hostplants: feeds on the pollen of various plants such as *Amaranthus*, *Solanum*, *Sonchus* and *Euphorbia*.

This is a pretty, delicate, extremely active little cricket. Its body and wings, in the short-winged forms, are black or nearly so, and the pale greenish-yellow hind legs form a striking contrast in color. The wings of the long-winged forms are brownish. The fully winged individuals are attracted to lights.

The identity of our material needs more detailed checking, I believe.

Subfamily ENEOPTERINAE

Tribe PROGATHOGRYLLINI (Perkins) new combination

Group *Prognathogryllides* Perkins, 1899:22.

The Hawaiian assemblage of peculiar and closely allied forms belonging to the Eneopterinae was considered by Perkins to be distinct enough to warrant the erection of a "new group" for them. Whether or not Perkins' "group" is worthy of being called a "tribe," or is enough isolated to be segregated and separately named requires further comparative study by a specialist in Orthoptera. All the genera and species are endemic to the Hawaiian Islands. The entire group evidently had its origin from a *Podoscirtes*-like immigrant allied to certain genera found from Fiji westward. The problem is in much need of review.

These are our most peculiar Orthoptera. All of them are flightless and all have extremely long antennae which are twice as long as the body or longer. The species are nocturnal and can be found hiding in the daytime in hollow stems, limbs, fern fronds and twigs, under dead bark, in clusters of dead leaves in trees, under moss, in dense clusters of ferns, at the bases of *Freycinetia* leaves and *Pritchardia* palm fronds, and in similar places. All the species are arboreal, and they are graceful and beautiful creatures when alive, but dried, shrivelled and misshapen museum specimens leave much to be desired.

Perkins saw drepaniid birds and the "oo," *Acrulocercus braccatus* (Cassin) (Meliphagidae), of Kauai feeding upon these crickets. No records of insect parasites have come to my notice.

KEY TO THE GENERA OF PROGNATHOGRYLLINI

1. Cerci about as long (male) or longer (female) than hind tarsi
..... **Prognathogryllus** Brunner.
Cerci distinctly shorter than hind tarsi..... 2
2. First fore tarsal segment shorter than segments 2 plus 3;
second tarsal segments dorso-ventrally depressed.....
..... **Leptogryllus** Perkins.
First fore tarsal segment as long as or longer than segments 2
plus 3; second tarsal segments laterally compressed.....
..... **Thaumatoeryllus** Perkins.

Genus **PROGNATHOGRYLLUS** Brunner, 1895:896

Aphonogryllus Perkins, 1899:26.

Nesogryllus Perkins, 1899:27.

Synonymy by Perkins, 1910:689.

The males have the tegmina well-developed for stridulation, and they may cover the whole abdomen, but the hind wings are rudimentary.

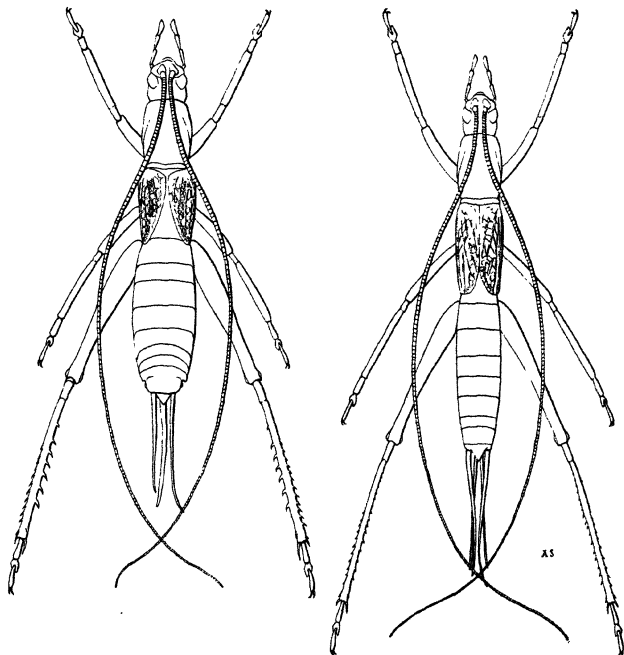


Figure 87—Holotypes of females of *Prognathogryllus alatus* Brunner, left, and *P. elongatus* Perkins, right. (Drawn at the British Museum of Natural History by Smith.)

Swezey found the eggs of a species of this genus inserted in the midribs of the leaves of *Labordia membranacea* on Mount Olympus, Oahu, in 1912. Egg 6×1 mm., cylindrical, curved near outer end, inserted at about 10 mm. intervals.

Hebard (1922 and 1926) considered that only *P. robustus*, *P. alatus* and *P. elongatus* were good species, but the types need careful study before any conclusions can be reached. Perkins (in letters) has said that he believes these species to be distinct and does not agree with Hebard.

Without a complete collection at hand, I shall not present a key to the species.

***Prognathogryllus alatus* Brunner (fig. 87).**

Prognathogryllus alatus Brunner, 1895:896, fig. 1; genotype, designated by Kirby, 1906:109. Perkins, 1899:24, pl. 2, figs. 8, 8a-b. Hebard, 1922:364, pl. 27, figs. 7, 8, extensive description and discussion.

Aphonogryllus apteryx Perkins, 1899:26, pl. 2, figs. 9, 9a-c, described from Oahu.

Endemic. Kauai (type locality: Waimea Mountains, 4,000 feet), Oahu.

Hostplants: *Clermontia*, *Pelca*, *Labordia membranacea* (eggs inserted in midribs of leaves; not the same record as listed above); lobeliads; in hollow fronds of *Cibotium* ferns.

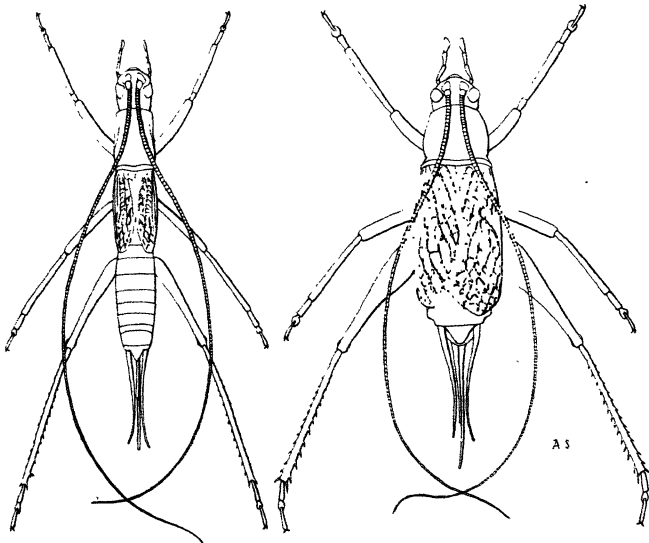


Figure 88—Holotype females of *Prognathogryllus inexpectatus* Perkins, left, and *P. robustus* Perkins, right. (Drawn at the British Museum of Natural History by Smith.)

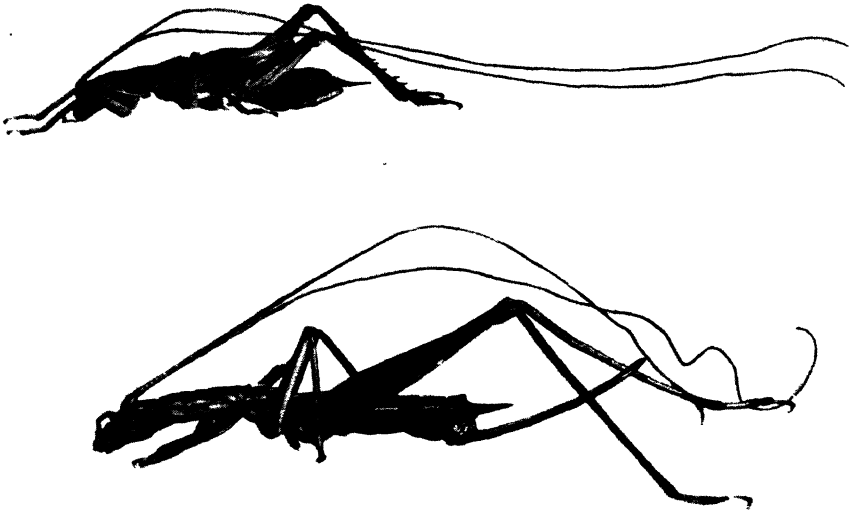


Figure 89—*Prognathogryllus oahuensis* Perkins, male, top (see dorsal view also); *Leptogryllus deceptor* Perkins, female, bottom. (Not to same scale.)

***Prognathogryllus elongatus* Perkins (fig. 87).**

Prognathogryllus elongatus Perkins, 1899:25, pl. 1, fig. 15.

Endemic. Kauai (type locality: the high plateau).

***Prognathogryllus inexpectatus* Perkins (fig. 88).**

Prognathogryllus inexpectatus Perkins, 1899:25.

Endemic. Kauai (type locality: 4,000 feet).

Found under bark.

***Prognathogryllus oahuensis* Perkins (figs. 89, 90).**

Prognathogryllus oahuensis Perkins, 1899:25. Hebard, 1922:368, pl. 27, fig. 9.

Nesogryllus stridulans Perkins, 1899:25, pl. 2, figs. 11, 11a; described from a unique male from 3,000 feet on Oahu.

Endemic. Oahu (type locality: Waianae Mountains); also recorded by Hebard (1926:302) from Kauai, Maui and Hawaii, but these records need checking.

Hostplants: *Touchardia* (in dead twigs), *Coprosma*, *Gunnera*, *Labordia*. Also found under bark.

***Prognathogryllus robustus* Perkins (fig. 88).**

Prognathogryllus robustus Perkins, 1899:25, pl. 1, fig. 14. Hebard, 1922:364.

Endemic. Kauai (type locality: the high central plateau, unique female).

Found in a cluster of leaves on a dead tree.

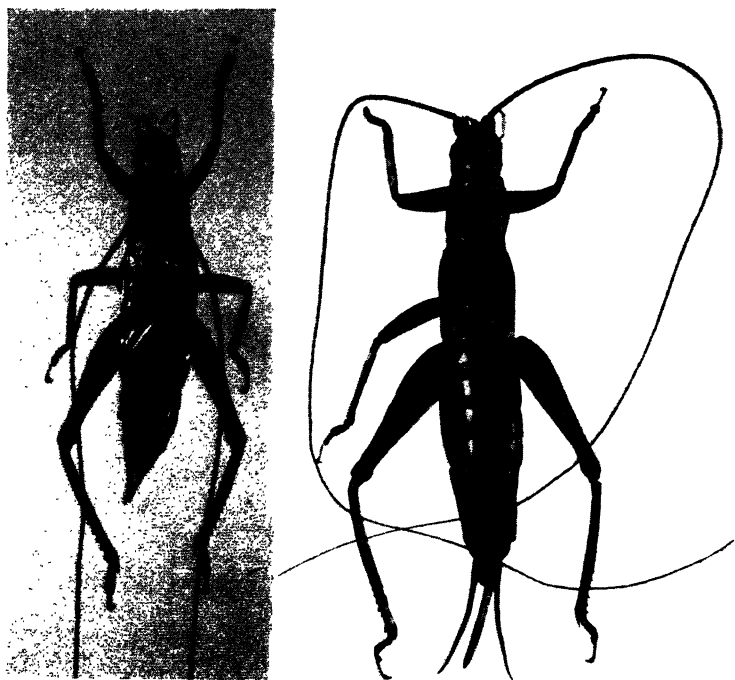


Figure 90—*Prognathogryllus oahuensis* Perkins, male and female (see also lateral view of male in previous figure). (Not to same scale.)

Genus **LEPTOGRYLLUS** Perkins, 1899:28

This genus is closely allied to *Prognathogryllus* and *Thaumatoeryllus* and has similar habits.

Hebard (1922:370), after studying a series of specimens, but not the types, came to the conclusion that there were only two or three species, instead of the eleven species included by Perkins. He said, "We believe that, of the eleven species described, most are synonyms, based on features which, though often showing marked differences, will be found on more thorough investigation to be valueless from a specific or even from a racial standpoint. In fact it may develop that but a single plastic species exists, breaking into many more or less intergrading phases."

Perkins does not agree with Hebard. I have been able to make a key which outlines some of the differences among the eleven forms named by Perkins, and I am inclined to agree with Perkins rather than with Hebard. Some of Perkins' names perhaps may not be good, but I am led to believe from an examination of some of his type and cotype material that there are a number of good species in this complex. Further critical study in connection with field work may reveal additional species.

As noted below, the types of three of the species are in the Bishop Museum, but the remainder are in the British Museum.

KEY TO THE SPECIES OF LEPTOGRYLLUS

1. Hind femora comparatively short, less than 7.5 mm. long.. 2
Hind femora 8.5 to 12 mm. long..... 4
- 2(1). Hind tibiae with about 10 or fewer spines along inner edge; Maui **simillimus** Perkins.
Hind tibiae with about 15 or more spines along inner edge:
Maui and Hawaii 3
- 3(2). Hawaii species **forficularis** (Brunner).
Maui species **similis** Perkins.
(Note: these may be the same species, but lack of material makes a decision impossible here.)
- 4(1). Hind tibiae conspicuously black for about the basal three-fourths of their lengths; Maui..... **apicalis** Perkins.
Hind tibiae not so colored..... 5
- 5(4). Hind tibiae with more than 30 spines in each dorsal row.... 6
Hind tibiae with less than 25 such spines..... 7
- 6(5). Tegmina extending back nearly to or beyond apex of metanotum and contiguous or nearly so.....
..... **nigrolineatus** Perkins.
Tegmina much smaller, extending only slightly behind mesonotum and widely separated, the distance between them greater than breadth of a tegmen.... **deceptor** Perkins.
- 7(5). A slender Kauai species; ovipositor unusually long (about 13 mm.), longer than hind femora; posterior tibiae with about 25 spines in the dorsal rows.... **cylindricus** Perkins.
Not such species, ovipositor shorter than a hind femora.... 8
- 8(7). Fore and mid tibiae conspicuously annulate..... 9
Tibiae not annulate 10
- 9(8). Kauai species; male tegmina concealing most of metanotum **kauaiensis** Perkins.
Oahu species; male tegmina reduced to minute flaps easily overlooked beneath hind corners of pronotum.....
..... **fusconotatus** Perkins.
- 10(8). Kauai species; male tegmina large and covering most of metanotum; female tegmina smaller, but extending about to apex of metanotum..... **nigromaculatus** Perkins.
Hawaii species; male and female tegmina small and leaving entire metanotum exposed, hardly extending behind mesonotum **elongatus** Perkins.

Leptogryllus apicalis Perkins (fig. 91).

Leptogryllus apicalis Perkins, 1910:689.

Endemic. Molokai, Maui (type series from both localities).

The male holotype is in the Bishop Museum.

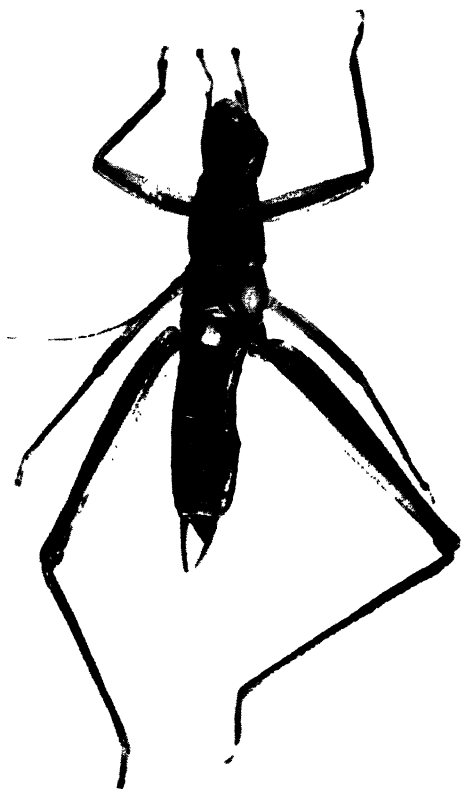


Figure 91—*Leptogryllus apicalis* Perkins, male.

***Leptogryllus cylindricus* Perkins.**

Leptogryllus cylindricus Perkins, 1910:688.

Endemic. Kauai (type locality: about 2,500 feet).

The male and female types are in the Bishop Museum.

***Leptogryllus deceptor* Perkins (fig. 89).**

Leptogryllus deceptor Perkins, 1910:689.

Leptogryllus decipiens Perkins (manuscript name, not published).

Endemic. Oahu (type locality: 1,500–2,000 feet).

The female holotype is in the Bishop Museum.

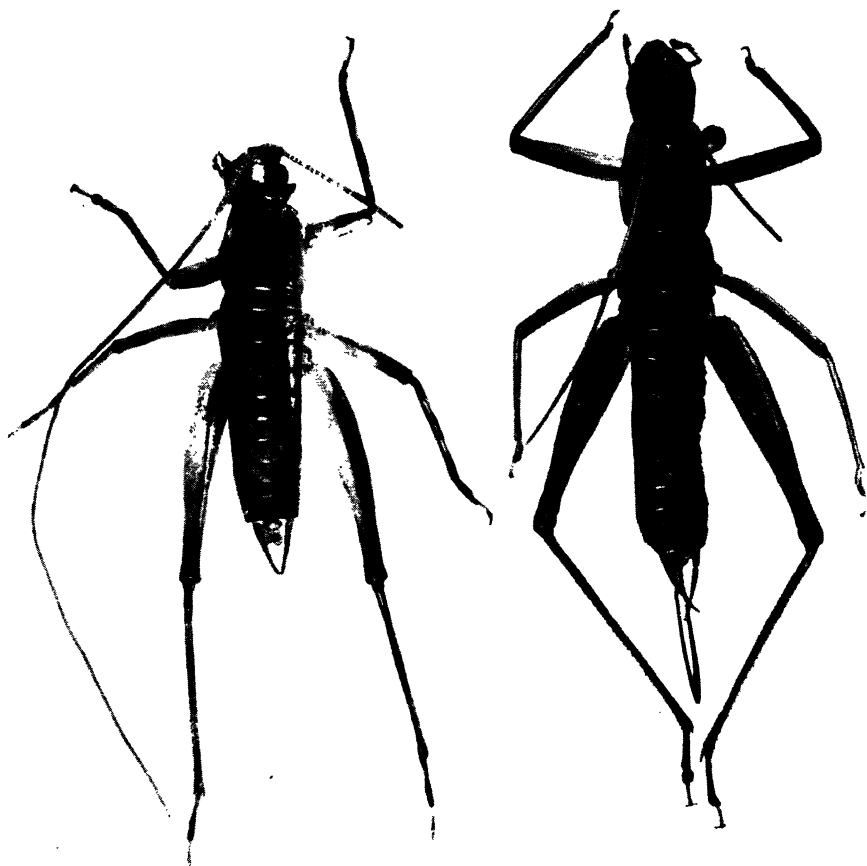


Figure 92—*Leptogryllus fusconotatus* Perkins, male, left; *Leptogryllus nigrolineatus* Perkins, female, right.

***Leptogryllus elongatus* Perkins.**

Leptogryllus elongatus Perkins, 1899:29, pl. 1, fig. 18.

Endemic. Hawaii (type series from Hilo, Puna and Kau).

***Leptogryllus forficularis* (Brunner).**

Prognathogryllus forficularis Brunner, 1895:897, fig. 2.

Leptogryllus forficularis (Brunner) Perkins, 1899:29, pl. 2, figs. 14, 14a-b.

Genotype; designated by Kirby, 1906:110. Hebard, 1922:372, pl. 27, figs. 10, 11.

Endemic. Hawaii (type locality: Kona, 3,000 feet) (Kauai?, Oahu?, Maui?).

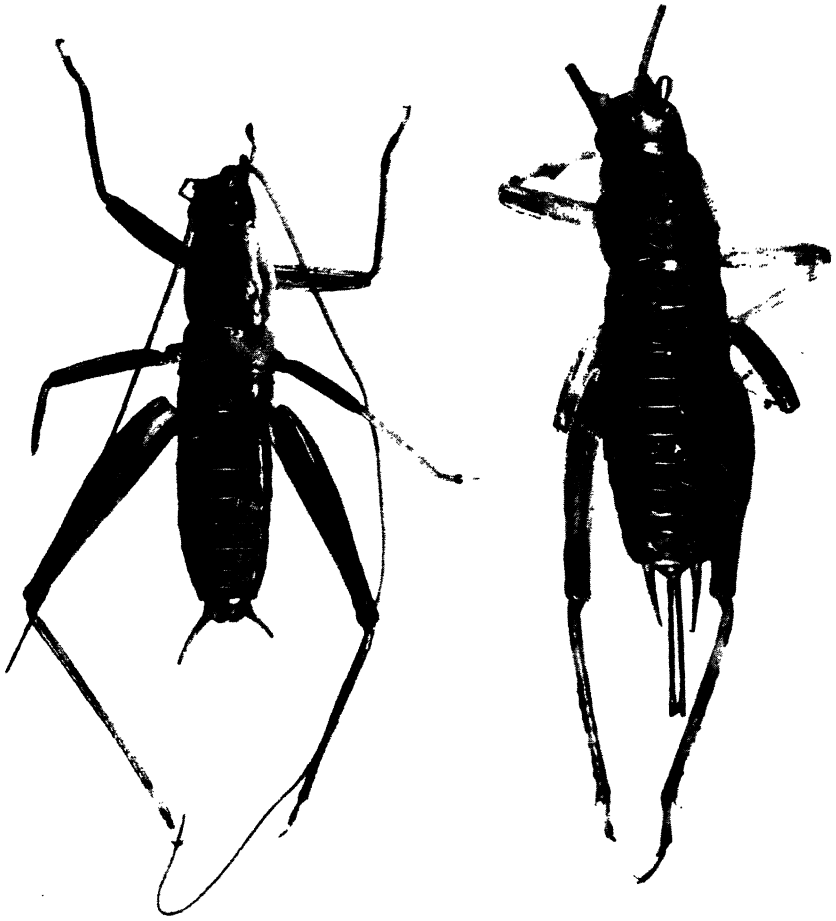


Figure 93—*Leptogryllus nigromaculatus* Perkins, male, left; *Leptogryllus simillimus* Perkins, female, right.

***Leptogryllus fusconotatus* Perkins (fig. 92).**

Leptogryllus fusconotatus Perkins, 1899:29.

Endemic. Oahu (type locality: 2,000 feet, unique male).

***Leptogryllus kauaiensis* Perkins.**

Leptogryllus kauaiensis Perkins, 1899:29.

Endemic. Kauai (type locality: 2,000–4,000 feet).

Leptogryllus nigrolineatus Perkins (fig. 92).

Leptogryllus nigrolineatus Perkins, 1899:28.

Endemic. Oahu, Maui, Hawaii (type series from mountains of Oahu and Maui).

Hostplants: at bases of leaves of *Freycinetia*, *Cibotium*.

Leptogryllus nigromaculatus Perkins (fig. 93).

Leptogryllus nigromaculatus Perkins, 1899:28, pl. 1, fig. 17; pl. 2, figs. 12, 12a.

Endemic. Kauai (type locality: 3,000–4,000 feet).

Leptogryllus similis Perkins.

Leptogryllus similis Perkins, 1899:28.

Endemic. Hawaii (type locality: above Hilo, 2,000 feet).

Leptogryllus simillimus Perkins (fig. 93).

Leptogryllus simillimus Perkins, 1899:30, pl. 1, fig. 19; pl. 2, figs. 15, 15a–b.

Endemic. Maui (type locality: 4,000–5,000 feet).

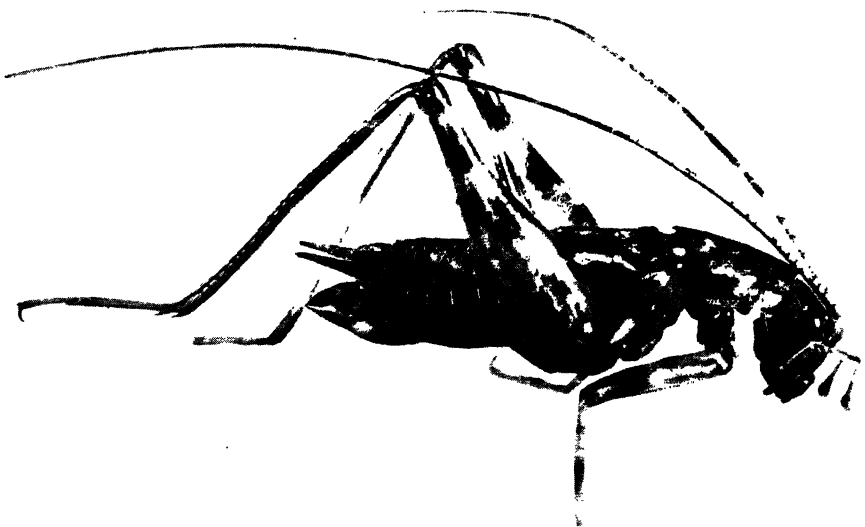


Figure 94—*Thaumtogryllus variegatus* Perkins, male.

Genus **THAUMATOGRYLLUS** Perkins, 1899:27

The specimens I have examined have the second tarsal segment laterally compressed, a character which, according to current keys to subfamilies, would exclude the genus from the Eneopterinae if used alone. To my knowledge, this character of the Hawaiian species has not been pointed out heretofore. However, this genus is obviously closely allied to *Prognathogryllus* and *Leptogryllus*, and I believe there is no doubt that all three genera have been derived from the same stock.

Thaumtogryllus variegatus Perkins (fig. 94).

Thaumtogryllus variegatus Perkins, 1899:27, pl. 1, fig. 16; pl. 2, figs. 10, 10a-d.

Genotype. Hebard, 1922:370.

Endemic. Kauai (type locality: 4,000 feet).

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Order ISOPTERA (Brullé, 1832)

(*isos*, equal; *pteron*, wing)

Termites, White Ants; Hawaiian name: "naonao lele"

Representatives of two of the five living families of termites are found in Hawaii. The primitive family Mastotermitidae and the families Hodotermitidae and Termitidae are not represented. All four of the termites found here are immigrants.

Compound eyes and two ocelli present in the alates, reduced or absent in other castes; antennae moniliform, inserted near the bases of the mandibles, multi-segmented, never much longer than the head; mouth parts generalized (or specialized in soldiers), exposed, masticatory; mandibles strongly developed, extraordinarily so in soldiers of most species, with two articulations with the head; maxillary palpi five-segmented, labial palpi three-segmented; wings (four) present only in reproductive castes, extending far beyond apex of abdomen, folded flat and superimposed over the back when at rest, subequal in size and shape, membranous, without obvious cross-veins in the Hawaiian forms, provided with a subbasal *fracture suture* along which line of weakness the wings may be broken off after the swarming flight (the stump left after the wings are shed is called the *wing scale*); legs similar, ambulatorial; tarsi three- or four-segmented in the Hawaiian forms (the proximal segments small and individually not very distinct in some forms); abdomen ten-segmented, cerci present, small, two-segmented; ninth ventrite with a pair of small cercus-like processes or tubercles in the male (styli); external genitalia not developed in the Hawaiian representatives; eggs deposited in nests, often in extraordinary numbers; nocturnal, xylophagous, soft-bodied, pale-colored (excepting the winged forms), social insects living in wood or soil with highly developed caste systems. Metamorphosis (incomplete) is least in the worker caste and greatest in the reproductives, and the change brought about from nymph to soldier is also striking. There are said to be five to eight molts.

The oldest fossils known are found in Eocene deposits, but these are already advanced, and a long prior evolution is presumed. The primitive Australian *Mastotermes* produces an ootheca and has other characteristics which show relationships to the cockroaches.

Termites are among the most unusual of all the Insecta. Moreover, they are among the most destructive groups of insects, especially in the tropics. About 1,800 species have been described. Although predominantly a tropical group, the distribution throughout the world roughly coincides with the 51° F. mean annual isotherm, which roughly follows the forty-fifth parallel of latitude in both hemispheres. Only a few genera are restricted to temperate regions.

Fortunately for Hawaii, we have only four species, but two of these species are unusually destructive and cause many thousands of dollars damage every year. Although everyone in Hawaii is familiar with the depredations of the group, our species are so insidious and cryptic in habit that little is actually seen or known of the insects themselves—excepting by those who are especially interested in them. We do not have any of the species which build spectacular exposed nests (*termitaria*) such as those found in Australia and elsewhere.

The highly evolved social system of the termites makes the colony an unusually efficient working population. The division of labor, and organization of the population and diverse morphological modifications of the various castes make these astounding animals among the marvels of creation. The social organization of termites might well serve as an ideal model for certain totalitarian human states. Within a colony of *Coptotermes*, for example, labor is carried out by certain individuals only. These individuals have their sexual systems underdeveloped or aborted, and their entire existence is guided by an unfailing instinct for continuous labor. The colony is guarded by highly specialized soldiers, also having aborted sexual organs, whose reason for living is to guard the colony from its foes. Their heads and mandibles are greatly or spectacularly enlarged for defensive action. *Coptotermes* soldiers have an enormous gland which occupies a large part of the body cavity and which produces a copious, sticky, milky fluid which is exuded when the soldier is disturbed. In *Nasutitermes*, which does not occur in Hawaii, the fluid can be squirted at will onto any foe from a gun-like tube opening in the forehead. The sexual forms tend only to migration, colony foundation and reproduction and are the only caste to have wings. In Hawaii the bodies of the reproductive caste only are pigmented and are more heavily sclerotized than those of the soldiers and workers, for members of the reproductive caste are the only ones who venture free into the outer world. Moreover, the eyes of the soldiers and workers are either greatly reduced or are absent, but the reproductives have well-developed compound eyes. Soldiers and workers include both sterile males and females, but whatever their basic sexual anatomy, both males and females act alike as soldiers or workers. The workers are the smallest individuals, the soldiers are somewhat larger, and the reproductives are the largest members of the colony. The duties of the workers are many: they forage for food, feed (by regurgitation) the young nymphs, soldiers and reproductives; they build the termitaria and runways and clean and maintain them; they tend the queen and store her eggs in "nurseries." The workers are absent in the primitive termites (*Kalotermitidae*), and their functions are performed by the nymphs of the other castes.

Swarming usually takes place in the spring and early summer. Unlike the swarming of certain Hymenoptera, Diptera and some other insects, the swarming of the termites is not a nuptial flight, for it has been found that mating does not occur until after a new home has been started. After the flight, the male and female join in a pair to found a new colony. Before they bore into wood or enter the soil, they shed their wings. The "fracture suture" at the base of each wing makes it possible for the wings to be discarded easily. The wings serve only to enable the

sexual forms to fly off in search of new colony sites. Once a new burrow is begun, wings are useless and would be a great handicap if retained. The wing-shedding mechanism is thus nicely adjusted to the mode of life of these creatures.

One of the most remarkable of evolutionary associations is the symbiotic relationship between termites (except the Termitidae) and certain kinds of Protozoa. So long has been this association of Protozoa and termites that we now find that allied groups of termites have allied protozoan faunas. Although our termites feed upon wood, they cannot digest sufficient cellulose by themselves. In their hind intestines, however, are seething masses of micro-organisms which include, among many other sorts of organisms, a complement of protozoans. These intestinal Protozoa are capable of breaking down the cellulose taken in by the feeding termite into materials, such as sugars, which the termite can assimilate. The termite thus builds its body tissue from food materials derived as by-products of the Protozoa it harbors in its intestine and from their dead bodies. By artificially removing the vital Protozoa from termites, it has been shown that, although the termites may continue to feed, they will starve in the midst of plenty. The carton material of a *Coptotermes* termitarium is rich in lignin, which is not used by the termites, but the woody material has had its cellulose removed. It is noteworthy that some wood-eating cockroaches also have intestinal Protozoa—some of which are said to belong to the same groups as those found in certain termites.

Dr. Harold Kirby has kindly examined fixed specimens of our termites and is responsible for supplying the names of the protozoans listed below under each of our species.

In most places in the world, remarkably modified insect guests—termitophiles—live in the nests and galleries of various termites. We do not have representatives of these highly specialized insects in Hawaii, however. There are a few apterygotan insects which are occasionally found with termites in Hawaii, but they are not restricted to such habitats.

Termites have many predators. Perhaps the most dangerous enemies to non-swarming termites in Hawaii are ants, several species of which attack termites whenever there is an opportunity. *Pheidole megacephala* is particularly likely to inflict heavy casualties. However, under normal circumstances the termites are well protected from attacks by ants, and it is usually only when some accident befalls a colony that it is exposed to attack by ants in Hawaii. At the time of swarming, the reproductives are most vulnerable to attack. If swarming takes place in daylight (as it does occasionally, although it normally takes place at night), dragonflies, skinks, mynah birds and sparrows gorge themselves on the flying termites. At night geckoes and *Bufo* toads take over the slaughter. Geckoes are particularly helpful in reducing the numbers which might enter houses by taking up their hunting stations on windows, screens and ceilings and capturing with insatiable appetites the swarming termites which are attracted to lights. The introduction of bats to Hawaii probably would aid greatly in the reduction of the numbers of swarming termites. The single native Hawaiian bat is rare and local in habit and

is not regularly attracted to the lowlands where termites are abundant. Pemberton (1928:147) found a lepismatid living in the nests and galleries of certain termites in Borneo and feeding upon the termite eggs and nymphs. A single attempt to introduce the species into Hawaii did not succeed because of the death of the small colony before the specimens could be released. No really useful methods of biological control of termites have yet been found. Artificial control is discussed under *Cryptotermes* and *Coptotermes*.

The reader is referred to the several general textbooks for a detailed account of the order.

TABULAR ANALYSIS OF THE HAWAIIAN ISOPTERA

FAMILY	GENERA	ENDEMIC GENERA	NON- ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Kalotermitidae	3	0	3	3	0	3
Rhinotermitidae	1	0	1	1	0	1
Totals	4	0	4	4	0	4

Fauna 100 percent adventive.

Average number of species per genus: 1.

KEY TO THE FAMILIES OF ISOPTERA FOUND IN HAWAII

1. Alates 2
Soldiers 3
- 2(1). Wings not hairy, radial sector with several distinct, anteriorly inclined branches, especially distinct toward apex; anterior wing scales very large and broadly overlapping hind wing scales **Kalotermitidae.**
Wings densely clothed with fine hairs, radial sector without branches; fore wing scales at most narrowly overlapping hind wing scales **Rhinotermitidae.**
- 3(1). Mandibles strongly toothed; frontal pore absent.
..... **Kalotermitidae.**
Mandibles not toothed; frontal pore conspicuous and from which is exuded a sticky, milky fluid. **Rhinotermitidae.**

A field character useful for distinguishing the two families in Hawaii is that the members of the Kalotermitidae produce characteristic sand-like fecal pellets (frass or "termite dust" or "termite sand" or "termite sawdust") which are to be found in quantities in their burrows and which are periodically cast out of the burrows (except in the mountain-dwelling *Neotermes*, in which species the pellets are not loose but are massed together). On the other hand, the excrement of the Rhinotermitidae is not produced in pellet form, but goes directly into the construction of nests and galleries. Thus, wood damaged by Kalotermitidae or dry-

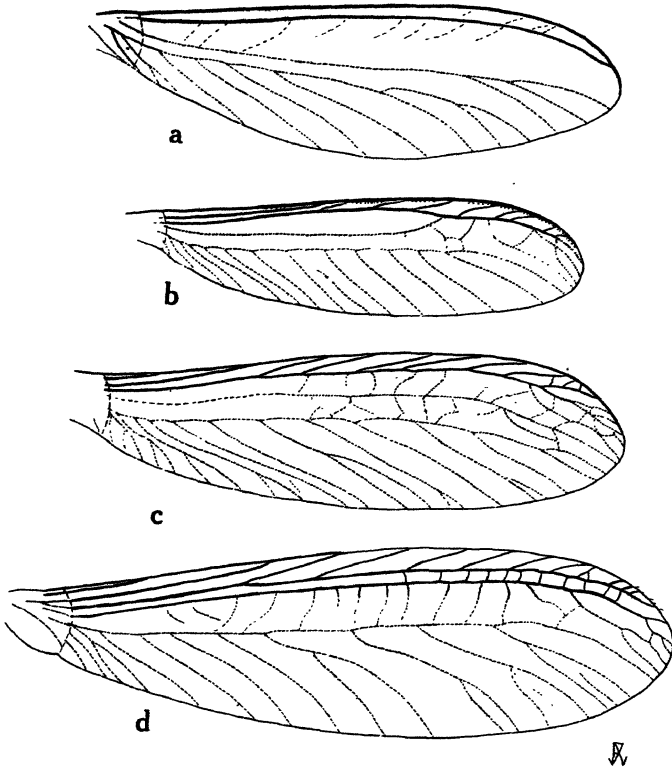


Figure 95—Sketches of fore wings of termites: **a**, *Coptotermes formosanus* Shiraki; **b**, *Cryptotermes brevis* (Walker); **c**, *Kalotermes immigrans* Snyder; **d**, *Neotermes connexus* Snyder. Note the subbasal fracture sutures. (From the original drawings by Williams, 1931.)

wood termites will be found to contain pellets, whereas wood tunneled by Rhinotermitidae will contain no pellets. Also, the Rhinotermitidae build carton nests and covered runways, neither of which structures is built by the Kalotermitidae. The workers of all forms having workers are closely similar (no true worker caste is found in the Kalotermitidae).

Family KALOTERMITIDAE (Enderlein) Banks, 1920

Calotermitidae Enderlein, 1909.

There are three species of this family found in Hawaii. One is a serious pest, but the other two are insects of field and forest. All three species are "dry-wood" termites. They can establish themselves in dry wood by boring directly through the surface and setting up a colony without access to soil moisture. Unlike *Copto-*

termes, the species of this family do not have a true worker caste, and the work is largely carried on by nymphs of the sexual forms. Unlike *Coptotermes*, the colonies of our species of Kalotermitidae are small—frequently not more than 100 individuals. On the other hand, the colonies may be numerous and the excavations of several colonies in the same piece of wood may overlap.

There has been confusion in the use of *Kalotermes* or *Calotermes*, and hence the varied spelling of the family name. The original spelling was with a "K," and because Opinion 34 of the International Rules of Zoological Nomenclature states that "Since evidence of the derivation of the word is not contained in the original publication, the original spelling . . . should be preserved" appears to apply in this case, the spelling should be *Kalotermes*.

KEY TO THE GENERA AND SPECIES OF KALOTERMITIDAE FOUND IN HAWAII

1. Alates 2
Soldiers 4
- 2(1). Fore wings with median vein heavily sclerotized (similar to radius), closely paralleling radial sector and with obvious branches to it; the largest Hawaiian species with breadth of head across eyes exceeding 1.5 mm. **Neotermes connexus** Snyder.
Fore wings with median vein very faint, not sclerotized as is radial sector; head less than 1.5 mm. wide. 3
- 3(2). Median vein of fore wings lying about midway between radial sector and cubitus and not curving up to join radial sector; head closer to 1.5 mm. broad than to 1.0 mm. **Kalotermes immigrans** Snyder.
Median vein of fore wings curving up to join radial sector near middle; head closer to 1.0 mm. broad than to 1.5 mm. **Cryptotermes brevis** (Walker).
- 4(1). Head short and squarish, its front conspicuously truncated, nearly vertical in front of antennae, the truncated vertical area concave and coarsely wrinkled as is dorsal area in back of declivitous region. **Cryptotermes brevis** (Walker).
Head not so formed, elongate, front gently sloping. 5
- 5(4). Third antennal segment longer than following two combined; pronotum about three-fourths as broad as long, its anterior margin broadly, deeply and conspicuously emarginate. **Kalotermes immigrans** Snyder.
Third antennal segment only about one-fourth longer than fourth; pronotum less than one-half as broad as long, its anterior margin shallowly concave. **Neotermes connexus** Snyder.

Genus **CRYPTOTERMES** Banks, 1906

This genus is found in both the Old and New Worlds and is known from Pleistocene fossils.

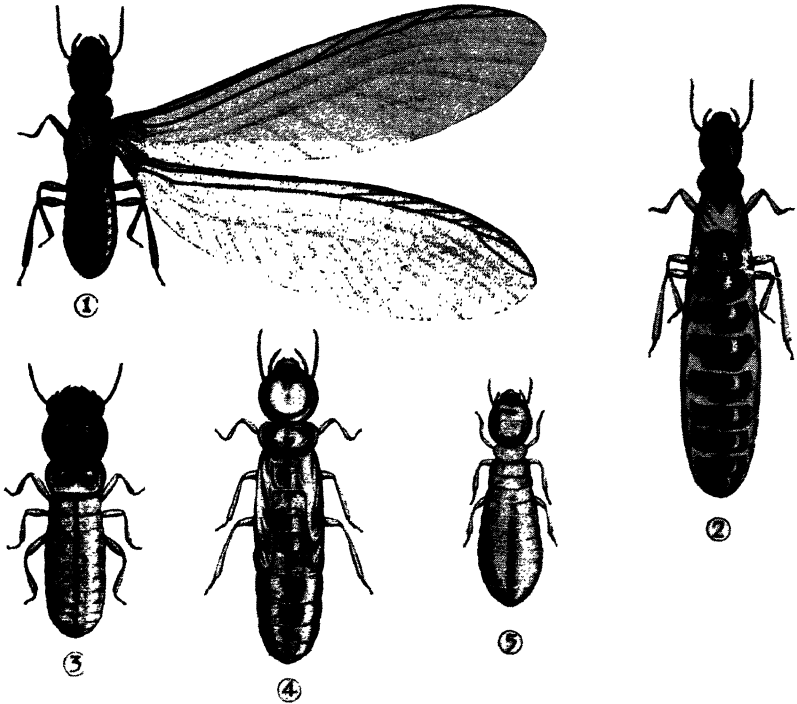


Figure 96—*Cryptotermes brevis* (Walker), the dry-wood termite. 1, winged adult; 2, dealtated gravid queen; 3, soldier; 4, full-grown nymph; 5, young nymph. (From a painting in the Board of Agriculture and Forestry, Honolulu. Courtesy of D. T. Fullaway.)

Cryptotermes brevis (Walker) (figs. 95b, 96, 97, 98).

Termes brevis Walker, 1853:524.

Cryptotermes piceatus Snyder, 1922:14, pl. 5, figs. 18, 19.

The dry-wood termite; powder-post termite.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii, Lisianski.

Immigrant. Tropical America, Florida, South Africa, China, Marquesas Islands. Evidently in Hawaii before 1869. A species widespread by commerce. Some of the early Hawaiian records of damage by *Kaloterms immigrans* really apply to this species.

Hostplants: probably most kinds of dry wood in houses and buildings. No detailed list of the kinds of wood attacked is available, but in addition to many kinds of wood commonly used in buildings and furniture, the termite has been found attacking *Grevillea robusta*, *Acacia koa*, *Eucalyptus*, *Nothopanax*, *Metrosideros* ("ohia lehua") and old redwood. It will bore through books, tar-paper and other materials.

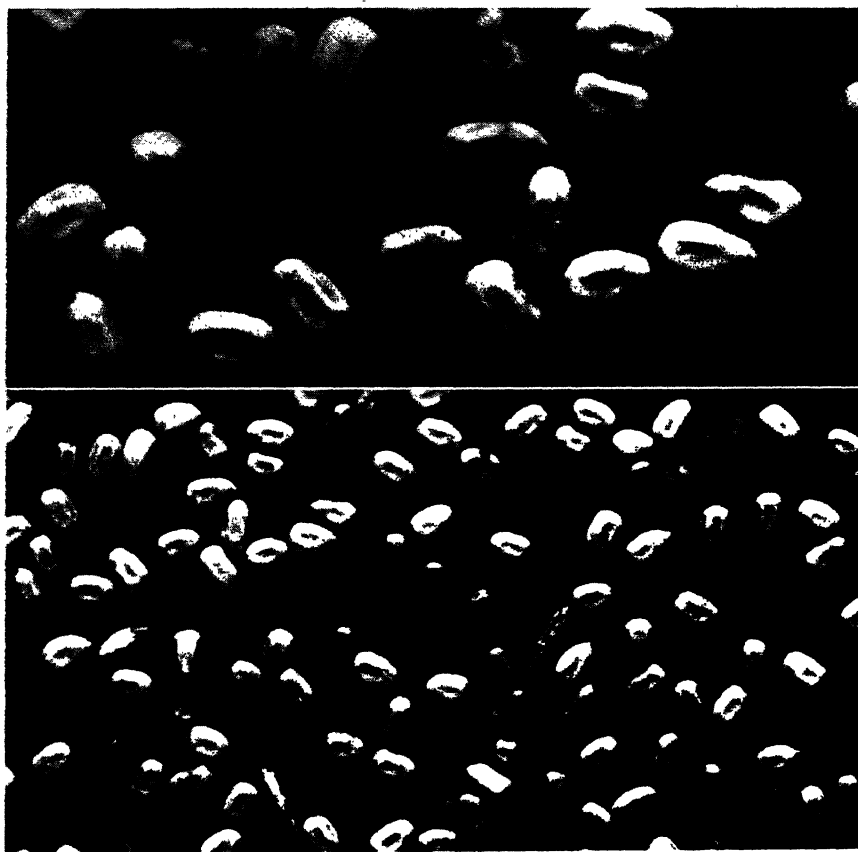


Figure 97—Greatly enlarged photographs of the fecal pellets of *Cryptotermes brevis* (Walker), the dry-wood termite.

Symbiotic flagellate protozoans: *Foaina humilis* Kirby (1942), *Devescovina striata* Foà (1905), *Tricercomitus divergens* Kirby (1930), *Hexamastix conclaviger* Kirby (1930), *Calonympha* sp. (probably *C. grassi* Foà, 1905).

This is a pest of the first order in Hawaii. It is the termite which so commonly damages wooden furniture of all kinds and may be found in almost anything made of wood. The annual damage done here amounts to hundreds of thousands of dollars. In founding a colony, the reproductives take advantage of any small crack, joint or hole (such as a nail hole) which they can find and commonly begin their tunneling from such a vantage point. After penetration is accomplished, the male and female tunnel along the grain of the wood, establish a nest and the female lays a few eggs. When the tunnels become crowded, an exit hole is bored to the exterior and quantities of the fecal pellets are pushed out. Such exit holes are closed with a brown parchment-like material. This habit makes the presence of the

termites known and is usually the first indication that an infestation exists in any article or situation. A focus of infestation is usually easy to locate directly above any pile of pellets. In houses and other buildings, infestations frequently begin in attics, and from there spread to all parts of the structures. Proper screening of all openings to attics will aid greatly in reducing infestations. Ehrhorn's (1934:302) recommendations for the control of this species are as follows:

Badly infested timbers or woodwork should be removed wherever possible, and the new timber or woodwork should be thoroughly treated with creosote or other substance before replacement. Slightly infested timbers or woodwork can be treated as follows with some success: Foundation timbers and timbers in unfinished attics, with creosote either with brush or spray gun; interior finish, such as door frames, window frames, floors, etc., with Paris green, powdered arsenic or sodium fluosilicate. In Hawaii we have had very good results with both methods. In treating an attic, we first use a vacuum cleaner, which removes all the pellets, dust, and other matter from the floor and other places. We then treat all visible infestations, either by the wet or dry method. After a week or two a reinspection is made, and wherever new droppings of pellets are found a close examination will reveal an over-looked infestation, which is then treated. Under such a system a thorough killing or extermination can be accomplished. The dry treatment, using Paris green or other poisonous material for interior finish, has given splendid results. In attics where the ventilators have been covered with fine mesh monel wire we find conditions better, with very few infestations, but where the ventilators are not covered the infestations are usually extensive.



Figure 98—A sketch of a burrow of *Cryptotermes brevis* (Walker) in a pine board. The point of entry of founders of the colony is the nail hole at the right.

When infestation occurs in furniture, the best possible method of control is to have the entire piece placed in a fumigating vault and thoroughly treated with cyanide, methyl bromide or similar fumigant. This method is, however, not always convenient or practicable to the individual homeowner, but larger institutions will save material and money by having a simple fumigating vault available. Entire rooms or whole buildings can be fumigated by experienced workers. With proper fumigation, the whole infestation in any given article can be destroyed in a single treatment. However, fumigation must be done carefully, and it takes long and thorough penetration to kill the termites deep inside the wood. Unbroken paint and varnish surfaces may be almost gas proof. Rapid, superficial fumigation will not give satisfactory control. In articles which cannot be fumigated without excessive effort or expense, the following method will give excellent results if applied properly. Ascertain the source of the termite pellets (an ice pick makes a good probe), and when the burrows are encountered, carefully make a small opening through the surface, then with a "puffer" or dust gun, blow in a charge of Paris green, sodium arsenite, sodium fluosilicate powder or other recommended poison dust. After treatment, the openings should be carefully plugged. If a colony has just begun, a single treatment may kill out the infestation. An entire colony may on occasion be exterminated by dusting only a single individual with poison. With

a good dust gun producing ample pressure, the dust can often be forced to almost all parts of a burrow system. Orthodichlorobenzene injected into the burrows with a hypodermic type of applicator is another recommended method of control. (Extreme care should be exercised with all such poisonous substances!) Wolcott (1945:444) found copper pentachlorophenate to be an effective "repellent" for use in protecting woods from attack by this species in Puerto Rico, and local workers who tried the material report good results. DDT has come into general use since this text was written, and it will undoubtedly be used extensively in control work.

This species has seriously damaged wooden frames and wooden parts of the tops of the older model automobiles in Hawaii. Damage was so severe to passenger and freight cars that the Oahu Railway and Land Company built a dry-heat chamber 75 feet long to use in controlling this termite. The temperature in the vault was raised to 150° F. by passing steam under 90 pounds pressure from a locomotive through radiator pipes lining the walls of the vault. Success was obtained with 1.5 hours exposure.

This species swarms usually in the spring, beginning on warm evenings and nights in May, particularly after rains. As a result of swarming, the number of colonies may be greatly increased in a building. Some property owners keep a low wattage electric bulb burning over a large pan of oiled water in their attics during the warmer months of the year. When the swarms emerge, the termites are attracted to the light, fall into the water and are drowned. This method will undoubtedly reduce the number of new foci of infestation. An effort should be made to keep termites from gaining entrance to buildings when swarming occurs. Open doors and unscreened or poorly screened windows and other openings through which the termites can fly when attracted to lights are commonly the sources of infestation.

Wood is not infrequently infested before it is used in construction, and care should be taken not to use old or second-hand lumber when there is a possibility that it contains colonies of *Cryptotermes*. Newly imported, freshly sawed lumber may easily become infested after delivery to the site of a new building, or it may become infested during fabrication. Moldings, window frames and cases, battens, stairways, floors, doors, ceilings, walls, underpinning, joists and other essential parts of houses are subject to attack and should be checked periodically.

This termite works in much smaller colonies and much slower than does *Coptotermes* and does not cause great damage in short periods of time. Its action is gradual and cumulative, and its attacks can be reduced to a minimum by vigilant care of property. Good paint and varnish finishes are deterrents to colony establishment.

The habits of this species make it easy to disperse, for it commonly infests packing cases, crating lumber, picture frames, boxes, barrels and wooden articles which are sent far and wide. The world will hear much more of this termite in the future than it has in the past, for it is sure to become widespread.

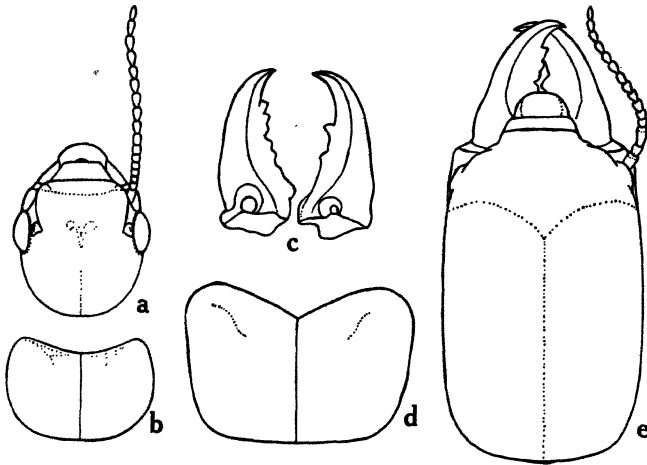


Figure 99—*Kaloterms immigrans* Snyder. a, b, head and pronotum of alate; c, d, e, mandibles, pronotum and head of soldier. All drawings to same scale. (Redrawn from Light, 1932:75.)

Genus **KALOTERMES** Hagen, 1853

Species of *Kaloterms* have been described from Oligocene, Miocene and Pleistocene fossils, and today the genus is widespread about the world.

Kaloterms immigrans Snyder (figs. 95, c; 99, a-e; 100).

Kaloterms immigrans Snyder, 1922:2, pl. 4, fig. 15.

Kaloterms marjoriae Snyder, 1924:3, pl. 1, fig. 6 (type locality: Hilo, Hawaii).

The lowland tree termite.

Kauai. Oahu (type locality: Honolulu), Maui, Hawaii.

Immigrant. Ecuador, and the Line, Marquesas and Galapagos Islands. First recorded from the Hawaiian Islands by McLachlan in 1883 (under the incorrect name *Caloterms marginipennis* Latreille).

Hostplants: common in many dead trees in the lowlands including *Acacia farnesiana*, algaroba (abundant, especially in the drier regions), *Eucalyptus*, *Gossypium tomentosum*, guava, *Hibiscus*, *Kadua*, *Lantana*, *Myoporum sandwicense*, *Nothopanax*, oleander; occasionally in fence and other posts, telephone poles and boards, but only under rare circumstances has it been found in buildings.

Symbiotic flagellate protozoans: *Tricercomitus divergens* Kirby (1930), *Coronympha clevelandi* Kirby (1929), *Trichonympha subquasilla* Kirby (1932), *Oxymonas* sp.

This is our second largest termite. It is especially abundant in algaroba groves, and it does not extend its range far into the mountains. The excrement is produced in characteristic loose pellet form.



Figure 100—Greatly enlarged figures of the fecal pellets of *Kaloterмес immigrans* Snyder, the lowland tree termite. Note the collapsed egg marked by the arrow in the lower figure.

Genus **NEOTERMES** Holmgren, 1911

Fossil *Neotermes* are known from Pleistocene deposits. The genus has a wide spread contemporary distribution.

Neotermes connexus Snyder (figs. 95, d; 101, a-e).

Neotermes connexus Snyder, 1922:9, figs. 3, 4; pl. 4, fig. 16.

Neotermes connexus variety *major* Snyder, 1922:11 (type from Kaiwiki, Hawaii); 1924:383, description of soldier.

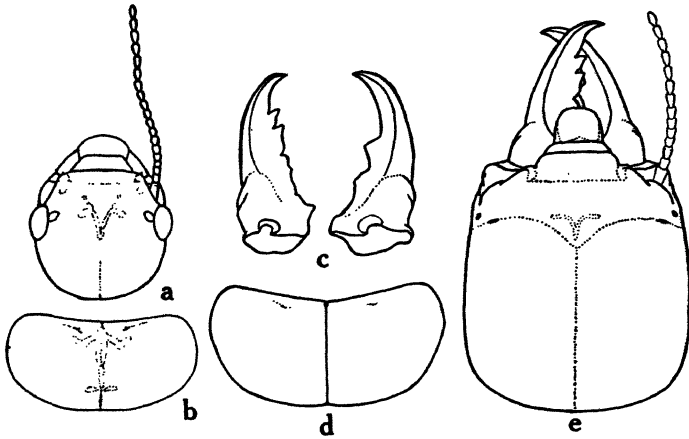


Figure 101—*Neotermes connexus* Snyder. a, b, head and pronotum of alate; c, d, e, mandibles, pronotum and head of soldier. All drawings to same scale. (Redrawn from Light, 1932.)

The forest-tree termite.

Kauai (type locality), Oahu, Molokai, Lanai, Maui, Hawaii.

Immigrant. Evidently widespread in the Pacific: Marquesas, Society, Samoa(?), Ellice (?), and Guam islands. First recorded from Hawaii by McLachlan in 1883 (under the erroneous name *Calotermes castaneus* Burmeister).

Hostplants: *Acacia koa*, *Broussaia*, *Byronia*, *Callophyllum*, candle nut, *Clermontia*, *Coprosma*, *Freycinetia*, *Gouldia*, guava, *Hibiscus tiliaceus*, *Lantana*, *Metrosideros*, *Pandanus*, *Perottetia*, *Pipturus*, *Straussia*, *Suttonia*, *Tetraplasandra*.

Symbiotic flagellate protozoa: *Foaina solita* Kirby, *Foaina gracilis* Janicki, *Foaina nana* (Kirby), *Devescovina hawaiiensis* Janicki, *Devescovina exilis* Kirby, *Parajoenia grassii* Janicki, *Tricercomitus divergens* Kirby, *Oxymonas granulosa* Janicki, *Stephanonympha silvestrii* Janicki.

This is the largest termite in Hawaii: the length of the alates may reach nearly 20 mm. It is typically a forest insect which may range from 500 feet up to about the 5,000-foot level. It requires a higher moisture content in the wood in which it lives than does either *Cryptotermes* or *Kaloterms*. It is common in dead stumps, logs, limbs and dead parts of living trees. Giffard recorded it feeding upon living wood of forest trees, but this and other such records are misleading, because the termites probably originally had attacked dead or decaying parts of the trees. The excrement of this species is not produced in loose pellet form; the pellets are massed in the excavations.

Pemberton (1928:149) recorded a parasitic nematode from the heads of specimens of this termite.

Family RHINOTERMITIDAE

Fortunately, only one species of this group of wood destroyers has gained entrance to Hawaii. However, the one species present does an enormous amount of damage every year.

Unlike the other termites found in Hawaii, the reproductive forms of *Coptotermes* cannot successfully establish themselves in perfectly dry wood. They must have plenty of moisture to carry on their vital processes. Also, unlike the *Kalotermitidae*, *Coptotermes* has a worker caste which is distinct from the working nymphs of the *Kalotermitidae*. The soldiers have a large and conspicuous frontal pore through which can be exuded at will a sticky, milk-colored fluid derived from an enormous gland which occupies much of the cephalic, thoracic and abdominal cavities. This fluid is used for defensive purposes—especially against ants.

These termites construct covered runways whenever they leave the ground or wood in which they are feeding in search of other food supplies. The covered runways not only serve to protect the termites from their enemies, but, most important of all, they enable the colonies to maintain the all-important high humidity essential for their well-being. Dr. Alfred Emerson, University of Chicago, informs me that they are “neutral” to light, and that they are not strongly negatively phototropic as is commonly believed.

Genus **COPTOTERMES** Wasmann, 1896

This genus has not been found in the fossil state, but species are now found in both Eastern and Western Hemispheres and are largely, but not entirely, confined to the tropics.

Coptotermes formosanus Shiraki (figs. 95, a; 102–109).

Coptotermes formosanus Shiraki, Trans. Ent. Soc. Japan 2:239, 1909. (I have not seen this reference.)

Coptotermes intrudens Oshima, 1920:262, pl. 7, figs. a–i (type locality: Honolulu).

The subterranean termite.

Kauai, Oahu, Lanai, Hawaii.

Immigrant. China, Formosa, Japan. First recorded from Hawaii by Swezey in 1913 when it was found in the chapel of Kamehameha School near Bernice P. Bishop Museum. However, Perkins had first discovered it in “1907 or earlier” in Honolulu.

Symbiotic flagellate protozoans: *Pseudotrichonympha grassii* Koidzumi, *Holomastigotoides hartmanni* Koidzumi, *Sperotrichonympha leidyi* Koidzumi.

The habits of *Coptotermes* make its distribution to widely separated localities less likely than that of *Cryptotermes*, which can be carried in almost any piece of dry wood. Therefore, *Coptotermes* has not become established on all of the main Hawaiian islands as has *Cryptotermes*. Some years ago some sprouted coconuts

from Oahu were transplanted on Maui. The damp husks of some of the coconuts were infested with incipient colonies, and the species became temporarily established on Maui. However, prompt attention resulted in the extermination of the localized Maui infestation. Small colonies of the species have been intercepted by plant quarantine inspectors at Honolulu in banana stumps from Manila and yams from Hongkong. The importation of potted plants from regions occupied by the termite is a great potential source of infestation, because small colonies may be established in the soil of the pots. The first record of the termite from Kauai was in 1928. On Lanai, careful attention has been given to the control and attempted eradication of the pest, and its distribution on that island is restricted.

The subterranean termite evidently first became established along the waterfront in Honolulu, and from there it has radiated outward. It has followed especially

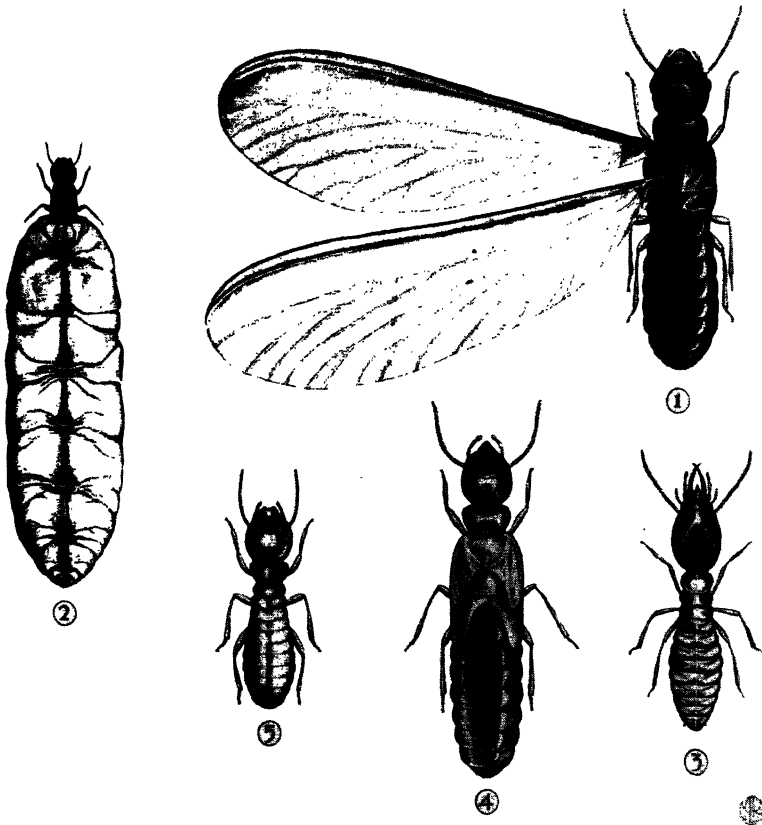


Figure 102—*Coptotermes formosanus* Shiraki, the subterranean termite. 1, winged adult; 2, gravid queen with body distended with ovaries and eggs; 3, soldier; 4, nymph of sexual or winged form showing developing wings; 5, worker. (From a painting in the Board of Agriculture and Forestry, Honolulu. Courtesy of D. T. Fullaway.)

utility pole lines and streetcar routes. Some observers believe that swarming individuals after being attracted to the lights of streetcars have been dispersed along the route by the moving cars. The infestations become noticeably fewer and fewer as one proceeds away from the center of Honolulu toward the mountains, but more and more reports are coming in from areas heretofore unoccupied by the termite, and it is obvious that it is still spreading.

No other insect in Hawaii causes as much damage to wooden structures as does this species. No estimates of the annual monetary losses are available, but they are great. Almost no kind of untreated wood or cellulose product is exempt from its ravages. When ample moisture is unavailable, the termites even turn to growing plants and are known to have damaged or killed many kinds of trees and sugarcane, corn, geraniums, *Coleus*, *Nothopanax*, *Bixa orellana* and other plants.

No detailed study has yet been published of the variety of materials eaten by this termite in Hawaii, but it is unusually wide. Oshima (1919) reported that teak (*Tectona grandis*) and Australian cypress pine (*Callitris robusta*) were immune to attack by this species. Camphor wood (*Cinnamomum camphora*), molave (*Vitex parviflora*) and ipil (*Intsia bijuga*) are comparatively resistant woods. In Honolulu old redwood in the ground (normally a fairly resistant wood), *Metrosideros* ("ohia lehua"), "Celotex," "Canec," "Masonite," coconut and a number of other woods and wood products have been reported attacked. Clothing and bolts of cloth, cotton, books, all kinds of paper, even heavily tarred paper, and such materials are damaged severely when accessible.

Optimum moisture is an absolute essential to this species, and when an adequate quantity is unavailable, the colony dies out. The species normally has a subterranean nest, but if a constant supply of moisture is available in buildings, even several stories above the ground, no contact with the soil is needed for a nest to be constructed. Nests are not infrequently found on the roofs of concrete buildings. These termites carry damp soil into their extended runways in order to maintain proper humidity. This habit often causes heavy growths of molds to grow in closed cabinets or closets which become infested, and the heavily infested parts of buildings may become musty-smelling.

Incipient colonies normally gain their start in or near the soil where adequate moisture and damp wood are available. The nests are normally built in the soil—usually at or near the bases of utility poles, tree stumps or near some other underground food source—but under favorable circumstances the nests may be found almost anywhere. Thus strong colonies may be established in boats, ships, barges, dredges, water tanks, piers or any similar place where moisture and cellulose are available. The structure of the nest is characteristic (see figures 105, 106) and is made of "carton." "Carton" is a term which has been applied to the friable substance constructed of soil and masticated woody substances cemented together by saliva and excrement of the termites. The runways are similarly constructed. The nests may be several cubic feet in size, and a single colony may contain several

hundred thousand individuals. The colony grows slowly at first, but momentum later is gained, and rapid increase sets in when the queen starts to lay as many as a thousand eggs a day. For a few to several days after pairing, no eggs are laid, then about two dozen eggs are deposited at the rate of one to four a day. The young queen then stops laying until her brood hatches (see Oshima, 1919). A mature queen is little more than an enormously expanded, fat, potato-like, egg-laying machine. She is locked in a "royal chamber" where she is at all times cared for by numerous "nurse" termites. If the queen dies, supplementary queens may develop within the colony under favorable conditions.



Figure 103—*Coptotermes formosanus* Shiraki. A gravid queen, 26 mm. long. The dark "islands" on the dorsum of the abdomen are the sclerotized tergal plates now greatly isolated on the ovary-distended abdomen.

The astounding numbers of active individuals in a mature colony can account for a surprisingly large amount of damage in a short time. It is possible to hear the termites working in wood if conditions are favorable. They snap their mandibles, especially if disturbed, and by tapping infested wood one may be able to hear clicking sounds.

Unlike the dry-wood termites, no telltale pellets are cast out of the burrows of this species. Hence, extensive damage can be done without any outward signs to warn the property owner. When improperly protected structures are built on heavily infested ground, truly remarkable amounts of severe damage may result in a period of a few months. I have seen parts of walls of a new dwelling hollowed out to mere paint-covered shells in three months' time. The feats of this termite in gaining entrance to buildings sound like "tall tales." They are known to make their way through brick walls, up through hollow-tile construction, through asphalt and asphalt-treated roofing materials, through defective concrete and even through lead sheathing. They will eat through almost any soft material to get at wood. A water hose left lying on the ground has been riddled. When these termites cannot burrow through a substance, they go around or over it by building their covered runways. They cannot go through brick or Portland cement, but they can pass through lime mortar. It is said that the soldiers pour out an acid secretion which dissolves lime mortar, and the grains of loosened sand are removed bit by bit.

The runways in the soil may extend over large areas, and an infestation at one place may have its origin in a nest 150 or 200 feet away. The subterranean burrows have been traced down as deep as 10 feet beneath the surface.

Flights in which thousands of reproductives from single nests take part are common in spring and early summer, and I have seen them as late as November. In Honolulu, major flights begin toward the end of March and extend to July, with the peak usually reached in May and early June. During this period extensive flights may be anticipated in the evenings of warm, sultry days—especially following rains. A heavy, warm rain is apt to bring out early swarms. Flights usually begin at sundown and end before midnight. Occasionally flights are reported in the late afternoon.

After swarming, the males and females pair off and set out to find a suitable place in which to found a nest. The wings are cast and the female leads a peculiar, nervous search for a possible nesting site. She runs about with the male following at her heels with his mouth parts and antennae at the apex of her abdomen. These tandems frequently appear to be single, elongate insects as they run this way and that. If they do not find moist conditions in which to settle down, they die. Specimens collected by me died in less than 24 hours when kept with wood in a dry glass.

The best way to prevent damage by *Coptotermes* is to build termite-resistant structures. With proper attention to structural details, this can be accomplished. Unfortunately, however, too little attention is given the termite problem before damage is apparent. Much money and time are wasted by treating damage after it is extensive, rather than adequately building against it. Unlike the dry-wood termite which is difficult or next to impossible to "build out," structures can be built which are proof against the subterranean termite.

There are several habits and requirements of the subterranean termite which, when interfered with, act decidedly in favor of the property owner and to the detriment of the termites. In the first place, the high humidity requisite to the colony prevents the establishment of subterranean termites in all except restricted situations. Any way that can be devised to eliminate the source of moisture will eliminate the colony. Colonies frequently become established on the roofs of high, reinforced concrete buildings when leaks develop and permit ample quantities of water to become constantly available beneath the roofing where there is some wooden material used in construction. Condensation in the walls, ceilings or attics of commercial buildings such as breweries and cold storage plants may provide favorable places for the establishment of vigorous colonies in the most unexpected places. Small leaks in water or sewer pipes which permit of a constant supply of moisture are also potential sources of colony establishment.

When subterranean termites reach an obstacle in their path, they build characteristic covered runways 5 to 10 mm. broad over the impenetrable obstruction to get to the food supply. By proper construction, it is possible to force the termites to build their runways in the open where they can be detected easily by routine, periodic inspection. Thus, every precaution should be taken to make it impossible for the termites to make a hidden entrance from the ground.

When termites die within the colonial structures, the corpses are devoured by their scavenging fellows. Also, termites not only clean themselves by using their

mouth parts, but they lick one another, and the queen, especially, is given a large amount of attention and is constantly fed and preened by her retinue. These habits make the use of poison dusts unusually effective, because a small amount of poison will frequently kill out an entire colony when applied to the bodies of a relatively few individuals. When Paris green, for example, is dusted into an inhabited gallery, the termites receiving the poison will not only lick themselves and thus become fatally poisoned, but other individuals will lick the dusted specimens, thus spreading the poison, and when the queen is fed she is apt to receive a lethal dose. When the poisoned termites die, the poison consumed by them is not entirely lost, because it is passed on to their fellows when the victims' bodies are consumed.



Figure 104—*Coptotermes formosanus* Shiraki. A stake used at the Bishop Museum for treatment of the subterranean termite as described in the text. Damage such as this may take place in less than six weeks. The top of the stake, which appears uneaten although it is hollowed out, protruded above the ground.

RECOMMENDATIONS FOR THE PREVENTION AND CONTROL OF DAMAGE BY *Coptotermes formosanus* IN HAWAII

A knowledge of the habits of subterranean termites will make many methods of control obvious. However, too little attention usually is given the problem by architect, builder and property owner before damage is evident. The time to think about termites and termite control is *before* a new dwelling or other structure is begun. Preventive measures should begin on the building site and blueprint.

A. Suggestions for the Prevention of Attack in New Construction

1. It is of the utmost importance that all wood and other cellulose materials be removed from the building site. All tree stumps and roots should be taken out. All scrap wood, shavings, large amounts of sawdust, stakes, boards from foundation forms and other such materials should be removed from the premises and not buried under soil fill or left around foundations or scattered about on the ground surface under any part of the building. Such materials left behind by construction workers make ideal sources of food for subterranean termites. All workers on new construction should be made aware that cleanliness is essential, and that all scrap wood and other such debris should be burned or otherwise removed from the premises. A Honolulu institution had a serious termite problem develop because boards used for forms for an extensive concrete retaining wall

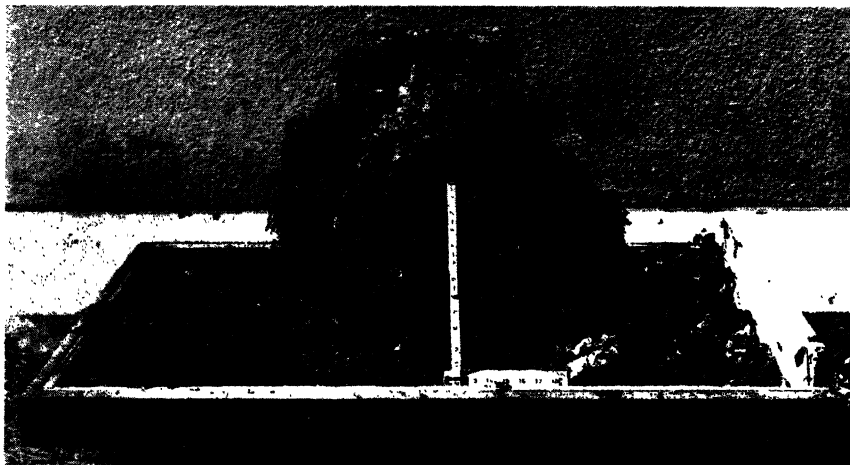


Figure 105—*Coptotermes formosanus* Shiraki. A nest built in a wooden box (size: 22 × 23 × 46 inches) which had rested on wooden planks on the ground in the basement of a building near the Bishop Museum for about a year (1937). The bottom was largely devoured, but the sides and top, although scored on the inside, were largely sound and not greatly eaten internally. The box was more than half filled with 46 pounds of friable nest structure which occupied about 6.5 cubic feet. (See also next figure.)

were left in the soil. This enabled large colonies of termites to build up close to the buildings and provided a major source of infestations over a long period of time. Every effort should be made to eliminate such food sources, because if such materials are unavailable the chances of building infestation are greatly reduced. If ample food supplies are available in the soil, large colonies may build up in the immediate vicinity of new construction and for years serve as a potential source of serious infestation. Although the building itself may be well insulated from the ground, some unforeseen circumstance may arise which will permit termites to gain entrance to the building.

2. If the new construction is built in an area known to be infested by subterranean termites, the soil may be treated with a poisonous chemical. Even if there are no subterranean termites known to occur on the property or near it, soil poisoning is a wise precaution. The United States Department of Agriculture (1942) recommends four principal chemicals for soil treatment which, it is said, can be expected to give at least five years' protection. These materials and suggestions for application are as follows:

Sodium arsenite (soluble in water; extremely poisonous). One gallon of 10 percent solution to every 5 cubic feet of soil treated is suggested by the Department of Agriculture. Randall and Doody (in Kofoid et al., 1934:472–483) consider a 10 percent solution too concentrated for safety. They believe that arsenicals should be avoided, but if they are used, the concentration should be 2 percent or less. They suggest 50 to 100 gallons of 2 percent solution for every 100 square feet of surface



Figure 106—*Coptotermes formosanus* Shiraki. A closer view of the nest shown in the preceding figure cut in half to show the internal structure.

treated. Mr. D. T. Fullaway (personal communication) has had success in Honolulu using about a 3 percent solution of this poison. It should be borne in mind that this is a very dangerous poison, and it should be used only in protected places. No plants will grow on soil treated with it, and the poison remains toxic for years. Moreover, any plants, even very large trees, whose roots are contacted by the solution may be killed outright. Trees as far away as 100 feet from a building being treated have been killed. Many experienced workers do not recommend its use because of the hazards involved. Under certain conditions, the arsenic may be attacked by bacteria with the resultant formation of deadly arsine gas (with a garlic-like odor).

Coal-tar creosote (insoluble in water; a skin and eye irritant). Use 1 part creosote to 3 parts of light fuel oil at the rate of 1 gallon to every 5 cubic feet of soil treated.

Orthodichlorobenzene (insoluble in water; the user should not get the chemical



Figure 107—Half-grown sugarcane ratoons damaged in the soil by *Coptotermes formosanus* Shiraki. This infestation was discovered on the grounds of the Hawaiian Sugar Planters' Association Experiment Station, Honolulu, after the main source of food supply of a colony of the termite was removed and the termites turned to the cane for food. (After Muir, 1917.)

on his skin nor breathe the confined vapors). It is suggested that best results may be obtained if a mixture of 1 part in 3 parts of light fuel oil used at the rate of 1 gallon to every 5 cubic feet of soil treated. This is a more expensive chemical, and it is perhaps best used in combination with coal-tar creosote. The mixture should consist of 1 part coal-tar creosote, 1 part orthodichlorobenzene and 6 parts light fuel oil and be applied as above. This chemical is a basic constituent of certain of the formulas employed by some commercial termite "exterminators."

Pentachlorophenol is used by some workers in a 5 percent solution in a light fuel oil (kerosene and light naphthas will only take up about 3 percent, however, and should not be used without the addition of a more active solvent). This material is also applied at the rate of 1 gallon to every 5 cubic feet of soil treated. The chemical can be purchased ready to use in a 5 percent solution.

McCauley and Flint (1942:23) recommend the following formula: Trichlorobenzene 2 parts and fuel oil 4 parts (by volume) applied at the rate of 3 gallons per 10 cubic feet of soil.

All of these solutions should be applied only beneath buildings where they will not affect shrubbery and are not readily accessible to human beings or pets. Reference should be made to the U. S. Department of Agriculture Farmers' Bulletin 1911 mentioned above, and to Kofoid et al. for detailed information. Great care must be exercised when poisoning the soil.

3. Ample clearance beneath all wooden construction is essential. Homes should be well-elevated from the ground. Every section of a house should be accessible

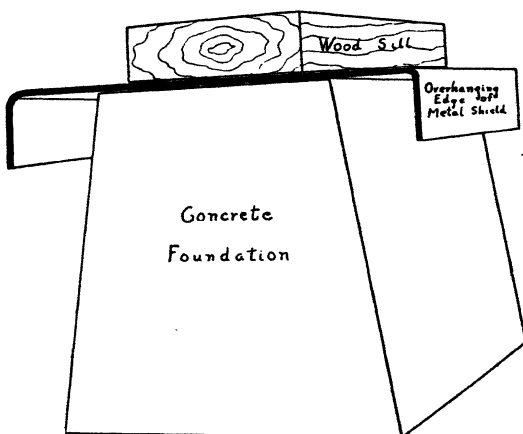


Figure 108—Diagram of cross section of a building foundation structure built to guard against attack by the subterranean termite. Concrete foundations are subject to cracking, and if a continuous metal shield is not laid between the concrete and the wood sill, infestation may occur by way of an undetected crack. The overhanging metal will bring any runways the termites may build over the foundation out into the open where they may be seen. (After Light, 1929:26.)

to permit proper inspection. In most places in Honolulu, a minimum clearance of two feet between floor joists and ground is recommended—and more is desirable. Ample provision should be made to keep the soil under buildings properly drained at all times, and adequate ventilator openings should be provided to insure a good circulation of air. Proper ventilation and drainage will go far toward reducing infestations.

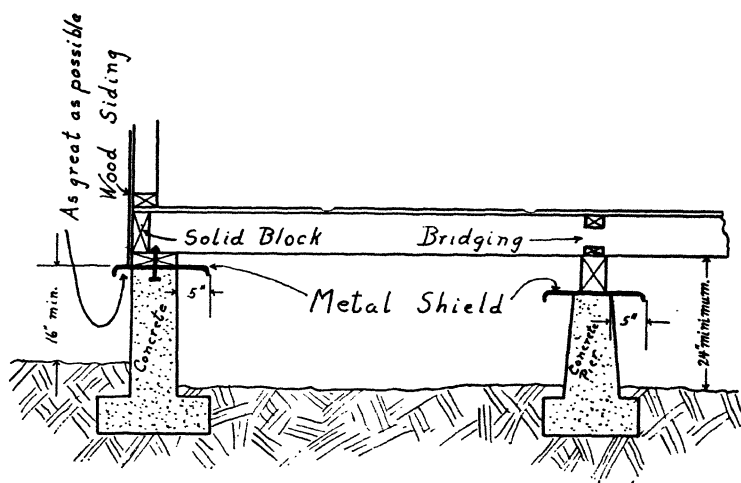


Figure 109—Suggested plan for building against possible attack by the subterranean termite. (After Light, 1929.)

4. The most important aid in the exclusion of termites is proper foundation construction. Unfortunately, much of the so-called termite proofing used in Hawaii is inadequate and improperly installed. Proper protection is not given by putting extensive metal caps on foundations and leaving the joints loose or leaving gaps at the ends. No timber should come in contact with the soil or be placed so near to it that the soil may, by washing in or otherwise, accumulate beneath it so that contact is established at any time after construction. All foundation walls or piers should be made of reinforced concrete. All such concrete foundations should extend at least six inches, preferably 12 inches, above the final possible level of earth or earth fill. All underpinning, sills, etc., should be separated from the foundation by noncorrodible metal shields. If it is necessary to have any wood come into contact with the concrete foundation, then it should be especially pressure-treated poisoned wood. It is advisable to have all underpinning made of pressure-treated poisoned wood. At least, all underpinning should be treated with two heavy coats of hot coal-tar creosote. Such treated wood is in itself not complete protection, however, because termites may extend their runways over it.

When treated wood is cut, the cut ends should receive two coats of hot coal-tar creosote. It is said that the wood treated with other than pressure methods will not give more than five years' protection, and it may become ineffective sooner than five years after treatment, especially in damp situations.

In Hawaii, many foundation walls and piers are constructed of stone and mortar. This type of construction is likely to crack and provide hidden termite entrances. Hollow cement tile and cinder-brick foundations are common but are also subject to cracking. Such foundation structures should be capped by metal shields. The following quotations concerning termite shields are taken from Farmers' Bulletin 1911 (U. S. Dept. Agr. 1942:27-32):

Recent experience has shown that the great majority of shields now in use have been poorly designed and incorrectly installed, giving the owner a false sense of security. The following are the mistakes most commonly observed where shields have been used:

1. Loose joints between sections of metal, often with no evidence of any attempt to solder or otherwise make a tight joint.
2. Improperly cut and soldered corners or angles where walls intersect.
3. Strip shields placed on top of foundations instead of being embedded in or attached to the side of the wall.
4. Anchor-bolt holes cut in bread-pan shields and not sealed with coal-tar pitch.
5. Insufficient clearance between the outer edge of the shield and adjacent woodwork or piping.
6. Shields less than 12 inches above grade line, sometimes even buried by grading operations.
7. Projecting edge of shields battered and bent out of shape, often flattened against piers or foundation wall.
8. Shields installed on sections of a foundation where there was little danger of termites attempting to gain entrance to the building, whereas the points of greatest danger, such as filled porches, were left unprotected.
9. Shields constructed of materials subject to rapid corrosion or to being easily torn or bent out of shape.

It should be remembered that shields, even when properly installed, will give protection only during the period that the metal lasts.

Recent laboratory experimental work with various types of termite shields has shown that no shield developed thus far is absolutely effective in preventing the passage of termites. A properly made and installed shield will, however, force the termites into the open where they can be seen and will thus act as an effective barrier to hidden attack. Termites may construct tubes on the lower surface of a shield, and occasionally one of these tubes will be extended around the edge and up over the upper surface. Frequent inspection for the presence of such tubes, therefore, is essential. If termites do succeed in getting past the shield, it may be necessary to apply a soil poison at the point where the colony is located.

The physical characteristics that appear to be requirements for an effective shield include at least the following:

1. The shield must be constructed of material that is impenetrable to termites. Copper or galvanized iron is most generally used.
2. The surface of the material must be smooth, i.e., slippery or polished, as any roughness makes it easier for termites to attach their tubes to it.
3. The outer edge of the shield should be as thin as possible. A smooth, thin edge makes it difficult for termites to extend their tubes from the lower to the upper surface of the shield and appears to be the most effective feature involved.
4. The projecting edge of the shield should be at least 2 inches from any other object and at least 12 inches above the ground. Termites will often extend their tubes out beyond the edge of the shield. If these free tubes come in contact with a wall, pipe, skirting, or other object that is connected with the structure above, the shield is rendered ineffective.

The bread-pan shield is especially suited for use over masonry walls or piers (stone, tile, brick, or hollow or solid blocks) that are not properly capped with 4 inches of reinforced poured concrete, to prevent termites from working through or between such units and reaching the structural timbers. The following describes their proper installation:

1. On interior walls and piers, extend the metal entirely across the top of the wall or pier and beyond it to project 3 or 4 inches on each side, with the outer portion bent downward at an angle so that the edge of the shield will have a clearance of at least 2 inches from any timber or other object.

2. On exterior foundation walls and piers the projection beyond the outer face of the wall may be reduced, as the wall surface is exposed and any termite activity can be readily detected. The same is true for the inner side of a wall around a full basement. However, the metal should extend far enough beyond the wall to allow a slight downward projection and to be readily inspected. If inspections are impossible or impractical, full projection should be provided, the same as for interior walls and piers.

When the spaces between exterior piers are closed with skirting or lattice work a minimum clearance of 2 inches must be provided around the edge of the shield, 1 inch between the sides of the skirting and the piers, and 2 inches between the lower edge of the skirting and the ground.

In all bread-pan shielding work the shield should be bedded on fresh cement mortar, coal-tar pitch, or coal-tar plastic cement, to seal any openings around the anchor bolts.

Utility pipes should not be neglected, because termites may follow them out of the ground to the building. Inverted funnel shields can be installed on most pipes entering a building and are a wise precaution. Pipes should be suspended from the building rather than placed on piers or wooden blocks on the ground beneath floors. Pipes passing through concrete should have tight flanges around them which are imbedded deeply in the concrete. A small crack will enable the termites to pass through walls or floors.

One particularly vulnerable point of attack is through lattice work or skirting closing off the under parts of houses. All lattice work should be kept clear of the ground and piers. Periodic inspection should be given to see that no soil has come in contact with the skirting (by gardening or other activities).

Shrubby along the sides of houses should be watched carefully, because a branch may provide a perfect route for termites to follow directly into woodwork. Vines growing up beneath houses or along lattice work frequently make access to the buildings possible. Accumulations of humus and dead leaves are not infrequently the entrance routes of subterranean termites. Absolute cleanliness of all areas beneath and immediately surrounding buildings should be the aim of every property owner interested in protecting his premises.

It is of utmost importance that careful routine inspection be made of the entire under parts of houses at least every year and preferably every six months in Hawaii. If your installation is properly constructed, all subterranean termite galleries will be forced into the open where you can see them. This point cannot be over-emphasized.

In the opinion of a number of workers in Hawaii, "termite bait stakes" should be an essential adjunct to termite protection of any dwelling or other building. It has been found that an ordinary pine or fir stake driven into the ground will be attacked in a short time if termites are working in the immediate vicinity. Thus, by discovering where termites are present in the soil, they can be killed out before they do damage. Termite bait stakes can easily be made of any clean, unpainted stock and should be about two inches thick and 18 to 24 inches long. The bottom

end should be pointed to facilitate driving. A deep groove about $\frac{3}{8}$ or $\frac{1}{2}$ inch wide should be cut in one side, and into this groove is placed a tight wooden strip so as to leave a hole down the middle of the stake (the same thing can be accomplished by drilling a hole for nearly the entire length of the stake, but that process is more difficult unless a long drill is available). It is important that the lower end of the hole be left closed, otherwise ants may gain entrance to the stakes and drive out the termites. These stakes are driven into the soil at intervals of 6 to 20 feet along the outside of buildings as well as under them, and corks or cotton wads are placed in the tops of the holes. The purpose of the hole is this: when the termites attack the stakes they will soon occupy the hollow (if the top is securely stoppered to exclude the light). An inspection can be made easily and quickly by removing the cork and examining the hole (a flashlight may be necessary). If the termites are in the hole they can be seen easily. When termites are found, a good poison dust should be blown into the interior of the stake. We have found this method effective in controlling termites which had gained entrance to reinforced concrete buildings and stone-walled buildings when it was impossible to locate runways through the walls. If hollow stakes cannot be had, an ordinary stake driven into the ground and periodically pulled out will serve a similar purpose. When termites are found in the stake, the holes in the ground as well as the damaged part of the stake should be dusted and the stake replaced. No dust should be applied to uneaten stakes—only infested stakes are to be treated.

Ehrhorn and other workers in Hawaii have used carbon bisulfide in connection with trap stakes with considerable success. When termites find the stake, it is removed carefully and a quantity of carbon bisulfide is poured into the hole which is then tightly covered. The confined gas will flow back along the termite tunnels and kill all termites with which it comes in contact. If the nest is close enough, the entire colony may be exterminated by the use of a single application—if luck is with you.

Termite bait stakes should be carefully inspected every two or three months. Whenever an infested stake is treated, it should be removed in about a week, the hole filled and a clean stake driven near-by—but not in the hole containing the poison. The author considers this method an excellent one, and surely it is one of the simplest, cheapest and easiest methods of controlling and preventing damage by subterranean termites. It is possible to keep large areas of ground free from termites by increasing the number of stakes used.

B. Suggestions for Treating Termite Infestations

In spite of all precautions taken, termite infestations sometimes do occur in the most unexpected ways and places. Therefore, the property owner should be informed on control of infestations. The most important thing to remember is that the subterranean termites cannot live in dry wood without access to moisture or moist soil. Therefore, if the line of communication between soil and the wood of your building can be broken, then all of the termites in the dry wood will die

and the infestation can be quickly eliminated. In buildings properly constructed against termite damage, it may be relatively easy to discover runways leading from the soil. However, in old structures or in certain buildings such as stores, factories, warehouses and similar buildings where necessity makes construction conform to certain plans, it is often difficult or impossible to find the source of infestation without the expenditure of such large sums of money as to make the attempt impracticable.

If damage is extensive, it will probably be best to call on a commercial firm specializing in such work, because the termites will not only have to be exterminated, but the seriously damaged parts of the building will have to be torn out and replaced.

If *Coptotermes* are found in a dwelling and the source of infestation cannot be ascertained, the woodwork being eaten should be carefully opened and some poison dust such as Paris green, sodium arsenite or sodium fluosilicate blown in at several places with a good dust gun. After treatment, the openings should be plugged. Dusts are not as effective in very damp wood. The finer the dust, the more efficient is its action. One treatment may eliminate the infestation, but subsequent infestation must be watched for. Although a colony may be killed out by dusting, if the soil about the dwelling is heavily infested, another colony may find its way into the same area via the same undiscovered route. Whenever such damage occurs, bait stakes should be set out under and around the dwelling.

Considerable damage may result in factories, warehouses and similar places by termites which have found their way through cracked concrete floors which have been laid directly on the ground, or through cracked walls below the soil surface. If the cracks are easily found they may be filled with coal-tar pitch. However, on occasion more expensive protective methods are essential. It may be necessary to kill out the termites which are nesting beneath extensive floor areas which cannot be adequately controlled by ordinary methods. Holes may be bored at 10-foot intervals over the whole area and a sodium arsenite solution can be pumped in to flood and poison the soil beneath the entire floor area. This has been done with success in Honolulu. On occasion, carbon bisulfide can be poured through similar holes to kill out infestations. When such expensive processes are required, and wherever possible, the holes should be fitted with capped pipes so that another poison application can be made at a future date if necessary.

Many old dwellings can be insulated from the ground by placing all underpinning and other sub-floor wooden structures on solid concrete blocks which have been capped with metal shields and making sure that there is no concealed route whereby termites may enter from the soil. It may be necessary to raise the entire structure off the ground. The whitewashing or white painting of all underpinning will facilitate locating the covered runways should any be constructed—especially in the darker places beneath buildings.

According to information given in Farmers' Bulletin 1911 of the United States Department of Agriculture (1942:37), the common practice of injecting chemicals into installed timbers and woodwork through bored holes has not proved successful.

The bulletin says, "Many attempts have been made to apply chemicals to wood in place in buildings, with the object of controlling existing termite infestations and preventing future damage. No effective control by spraying or fumigation has proved to be possible. It is not considered practical to secure effective penetration by injecting chemicals under pressure through bored holes without boring so many holes that the strength of the timber is seriously weakened. Such methods of control are therefore not recommended." The spraying of chemicals upon wood surfaces has proved to be an unsatisfactory procedure; it is a "snare and delusion."

Before closing this chapter, it is perhaps advisable to caution the property owner to be careful in selecting "termite exterminators" or commercial insect control companies. Much money can be wasted in having poorly trained workers or unreliable firms treat your property. Some workmen can be depended upon to give honest and good service, but the public's lack of knowledge of entomological work in general leaves the way open for exploitation. Some methods and materials used by commercial exterminators have been proved worthless or of little permanent value. However, a reliable firm can do much to aid in the control of insect pests on the premises.

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Order **EMBIOPTERA** Shipley, 1904

(*embios*, lively; *pteron*, wing)

Embiids, Embiopterans, Webspinners

Elongate slender insects; head large, free and completely exposed, prognathous, broader than the prothorax; antennae larger than the head, multisegmented (about 16–20 segments in our species); compound eyes reniform, well developed, conspicuous, larger in the male than female; ocelli absent; mandibles large, well developed, dentate, larger in the male; maxillary palpi five-segmented; labial palpi three-segmented; four similar membranous wings of nearly equal size and shape present on the male only, folded flat over the pterothorax and abdomen when at rest, with few cross-veins, the insertions of the fore wings widely separated from the insertions of the hind wings; abdomen with ten complete tergites in the female, nine in the male with the tenth asymmetrically divided; with eight complete and fully exposed ventrites, the first and terminal sternites modified or not very evident; female genital opening between sternites eight and nine; male terminalia peculiarly asymmetrical; cerci two-segmented (in our species), asymmetrical in the male; ovipositor wanting; legs with the hind femora enlarged; tarsi three-segmented, the first segment of the anterior pair conspicuously expanded in all stages to hold highly modified spinning glands; claws paired, divergent; hind tarsus with bladder-like protuberances on the soles of the first two segments, middle pair of legs less strongly developed than the others; eggs deposited in groups attached to walls of the tunnels, opercula large and conspicuous; metamorphosis slight, incomplete; nocturnal, soft-bodied insects living in silken tunnels usually beneath objects lying on the ground, under dead bark or in leaf mold.

Only a single representative of this peculiar order occurs in Hawaii, and it is an immigrant.

Fossil Embioptera are known from the Tertiary, and the extinct family Protembiidae has been described from Permian beds. The present geographical distribution of the order is largely tropical, and the north and south limit is between the fortieth and forty-fifth parallels of latitude. There are about 150 species known, and the greatest diversification of the order today appears to be in Africa.

Among all the orders of insects, the Embioptera are unique because of their highly developed tarsal silk-spinning glands which are used to produce great quantities of silk to construct the ramifying galleries in which they live. The only other known insects which have tarsal spinning organs are certain empidid flies, but their silk is used to envelop prey. Embioptera can probably be looked upon as the most efficient of insect silk-makers. All species of the order including both sexes and all instars produce silk.

Mills' (1932:651) description of the spinning habits of the American species *Anisembia texana* (Melander) is worth quoting:

The Embiid's enlarged metatarsi (fore basitarsi) bear a great resemblance to a pair of boxing gloves, and as it swings them about in front of itself in spinning a web, it reminds one of a miniature prize-fighter shadow-boxing. As the feinting continues a fine haze is seen to appear in front of the spinner. Against a light background the fine web is all but invisible and, as the Embiid pushes out on it, it appears to be walking through space. By spinning as it slowly rotates on its long axis, the characteristic silken tunnel is produced. Within this tunnel it seems to pay no attention to gravity, being found as often as not with its ventral side upward. It moves with alacrity both forward and backward in the web. As it moves or hangs in the web, the first and last pairs of legs hook into the web naturally while the middle pair extends over the back, attaching to the portion of the tunnel which is just behind the dorsum; in other words, if the insect is standing in the tunnel with its ventral side down, the middle legs extend upward over the back, hooking into the silk above, but bearing little of the weight of the body. This may account for the comparative reduction in the size of the femora of the middle legs.

All known females are wingless and are little more than sexually mature nymphs. Some genera also contain species in which both males and females are wingless, and other species may have both winged and wingless males. The wings are soft, pliable and tissue-like and are easily crumpled as the males move about in their galleries. Ross (1940) believes that the wings are made rigid for flight by the maintenance of blood pressure in the large radial vein.

The species are usually gregarious and several to many individuals may be found inhabiting a common and extensive system of silken galleries. The eggs are given a primitive sort of attention by the female, who seems to stand guard over them until they hatch, and the young nymphs appear to stay near their mother.

A remarkable and unusual habit of these insects is their ability to run backward as well as forward. When disturbed, they can run backward through their tortuous galleries with surprising speed and evidently with no more difficulty than their forward motion. An interesting anatomical modification has taken place in the enlarged hind femora to make this backward motion possible. Contrary to the usual form of muscle arrangement, the depressor muscle is much more developed than is the levator muscle to the tibia.

Suborder EUEMBIOPTERA Davis, 1940:677

Euembia Tillyard, 1937.

The suborder Protembioptera is known only from Permian fossils, and the suborder Euembioptera contains one fossil and six living families.

Family OLIGOTOMIDAE Enderlein, 1909

This family is naturally restricted to the Old World, but some of the species have been spread by commerce to both hemispheres. The hemitergites of the tenth tergite of the male are not distinctly separated by a membrane, the radial sector has three branches, the mandibles have apical teeth, and the two-segmented left cercus of the male is not echinulate on the inner side.

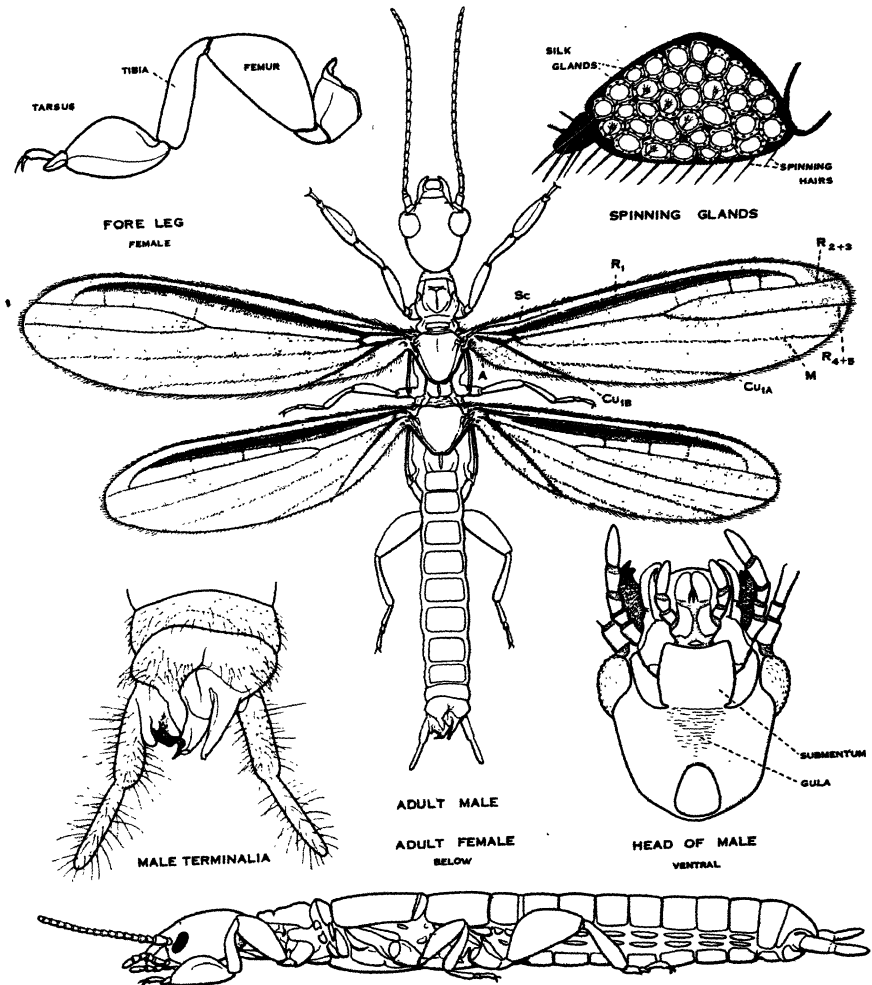


Figure 110—*Oligotoma saundersii* (Westwood). (Plate prepared especially for this volume by E. S. Ross, California Academy of Sciences.)

Genus **OLIGOTOMA** Westwood, 1837:373

This genus is native to the Indo-Australian regions, but some of its members have been widely dispersed artificially through the tropical and subtropical parts of the world. The species found in Hawaii is:

Oligotoma saundersii (Westwood) (figs. 110, 111).

Embia (subgenus *Oligotoma*) *Saundersii* Westwood, 1837:369, figs. 2, 2a-2f (type from Bengal). Genotype.

Embia Latreillii Rambur, 1842:312 (type from Madagascar).

Oligotoma insularis McLachlan, 1883:227 (type from Hawaiian Islands).

Oligotoma Cubana Hagen, 1885:141 (type from Cuba).

Oligotoma bramina Saussure, 1896:352 (type from Bombay).

Oligotoma hova Saussure, 1896:354 (type from Madagascar).

Oligotoma rochai Navas, 1917:281, fig. 17 (type from Brazil).

Oligotoma inaequalis Banks, 1924:421 (type from West Indies).

Davis (1939) and Ross (1940) give figures and extensive discussions of this species and these are referred to the interested student. Davis (1939) gives a long list of the many localities from which the species has been reported.

Kauai, Oahu, Molokai, Maui, Hawaii, Kaula, Nihoa, Necker, Laysan.

Immigrant. Widespread by commerce to many tropical and subtropical parts of the world from Africa to eastern Polynesia and to North and South America. First recorded from the Hawaiian Islands by McLachlan (as *O. insularis*) in 1883.



Figure 111—*Oligotoma saundersii* (Westwood). Male, left; female, right; not to same scale. (Photograph of female supplied by E. S. Ross.)

Parasite: *Mystrocnemis vagabundus* (Bridwell) (Hymenoptera: Sclerogibbidae).

This species is common in Hawaii and is most abundant in the drier lowlands. It has been found in dry areas up to 3,000 feet, however.

It can be discovered in its extensive webblings beneath old boards and other such articles thrown out on grass or leaves especially, under dead bark, under stones, particularly if they are on decaying vegetation, in dead matted vegetation, in hollows in branches, in ground litter and in similar situations. Its food consists of dead vegetable matter, and perhaps it eats fungi also. I have kept the species alive in damp leaf mold in the laboratory for many months. The males are attracted to light. Ross (1940) gives an ample redescription of the species and a detailed bibliography. Perkins (1897) and Kershaw (1914) give notes on the development.

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Order **DERMAPTERA** Leach, 1815

(*derma*, skin; *pteron*, wing)

Earwigs; Hawaiian name: "lo"

Body elongate, depressed, well sclerotized, leathery; head large, exposed, subcordate, prognathous; mandibles large, masticatory, dentate; maxillary palpi five-segmented; labial palpi three-segmented; antennae elongate, filiform, multisegmented, longer than the head and prothorax, with 10 to about 50 segments; compound eyes well developed; ocelli absent; wings present or absent, when present the fore pair reduced to veinless, abbreviated, leathery tegmina shorter than the abdomen and similar in appearance to the elytra of staphylinid beetles; hind wings peculiarly developed, semicircular, the vanal area greatly enlarged, with modified, radiating veins arising from rather extensive sclerotized anterior and basal areas, folding fanwise longitudinally and twice transversely for storage beneath the tegmina; legs ambulatorial, widely separated; tarsi three-segmented, claws paired, free, empodium present or absent; abdomen largely exposed, telescopic, 11-segmented, first and last tergites modified, concealed or indistinct, male with nine

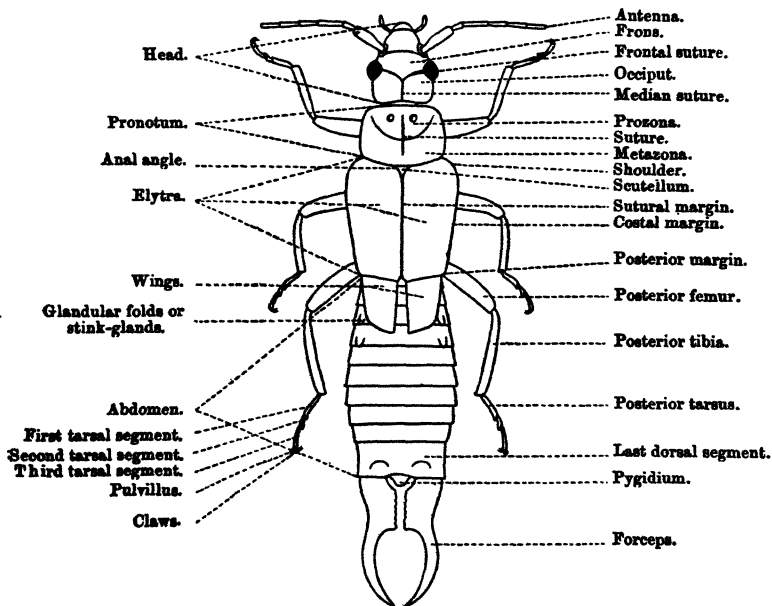


Figure 112—Diagram of dorsal aspect of an earwig. (After Burr, 1910.)

tergites visible, female with seven; males with eight visible ventrites, females with six; cerci unusually large and conspicuous, modified in the adult into large, strong, conspicuous, heavily sclerotized, unsegmented forceps, often armed with teeth; ovipositor wanting; metamorphosis slight; eggs of most species laid in batches in nests usually in the soil or under objects on the ground or in protected places in the ground or in vegetation or under bark or in debris; four to six molts; mostly nocturnal, omnivorous or mostly carnivorous dwellers of moist places and easily recognized because of their conspicuous forceps, short tegmina, unconventional wings and exposed abdomen.

Fossil Dermaptera are known from as far back as the Jurassic. Today the order is represented by approximately 1,000 living species, most of which are tropical insects.

Imms (1934:252) says, "The term 'earwig' possibly took its origin from the fact that these insects have been known to use the human ear for purposes of concealment; on the other hand it has been suggested that the word is a corruption of 'earwing' in allusion to the form of the hind-wings."

The forceps are used for various purposes by different species. Most species use them in capturing or holding insect prey and for defense and fighting. Some are reported to use them during copulation, or to aid in folding the wings; some

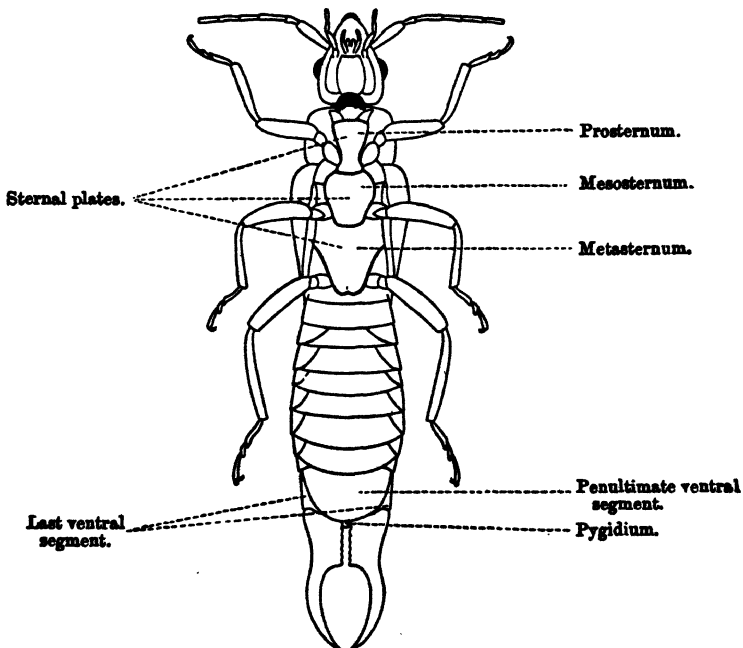


Figure 113—Diagram of ventral aspect of an earwig. (After Burr, 1910.)

observers report that certain species do not use their forceps for copulation or for folding their wings. Some species can pinch hard enough to draw blood from a finger. Most observers report that the movements of the insects and the action of their forceps in capturing prey are "lightning-like."

One of the unusual habits of the earwigs is the care given the eggs and young by the female. After the eggs are deposited, the mother earwig crouches over them in a manner suggestive of a setting hen and, after the eggs have hatched, cares for the young until they are ready to forage for themselves.

The peculiarly formed hind wings of earwigs are unlike those of any other group of insects (see fig. 117).

Although there have been several species described from Hawaii, and some species are known only from the islands, it appears that all are immigrant species, and that Hawaii is without an endemic earwig fauna.

The species found in Hawaii are considered generally as beneficial insects, but some species found elsewhere are pests of economic importance.

The order is a taxonomically difficult one, and the student may have difficulty identifying his material. The variation within the species is great and confusing.

The characters used in the keys in this section apply to the species found in Hawaii only and may not be applicable for the separation of other genera and species. I have attempted to use characters most easily seen by the non-specialist and student.

TABULAR ANALYSIS OF THE HAWAIIAN DERMAPTERA

FAMILY	GENERA	ENDEMIC GENERA	NON- ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Labiduridae	3	0	3	4	0	4
Labiidae	3	0	3	5	0	5
Chelisochidae	2	0	2	2	0	2
Totals	8	0	8	11	0	11

Fauna 100 percent adventive.

Average number of species per genus: 1.3.

Suborder FORFICULINA Newman, 1834

The only other suborder is the Arixenina, which includes aberrant insects which are ectoparasitic on, or otherwise associated with, bats. None of these peculiar insects is found in Hawaii.

KEY TO THE FAMILIES OF DERMAPTERA FOUND IN HAWAII

1. Second tarsal segment produced into a conspicuous lobe under, and extending for about half-way beneath, the third segment (examine from the side).....**Chelisochidae.**
- Second tarsal segment either simple or bilobed but not produced beneath the third 2

2. Pygidium vertical and concealed from view or almost concealed from directly above; antennal segments four to six, inclusive, shorter than, or at most as long as, first plus second, segment six less than twice as long as broad (be sure to measure across the broadest side).....**Labiduridae.**
- Pygidium visible from above, usually broadly exposed; antennal segments four to six inclusive much longer than first plus second, six always twice or more than twice as long as broad**Labidiidae.**

Family LABIDURIDAE Verhoeff, 1902

KEY TO THE SUBFAMILIES FOUND IN HAWAII

1. Posterior margin of the mesosternum conspicuously arcuate; wings and elytra normally absent in our species.....**Psalinae.**
2. Posterior margin of the mesosternum subtruncate; wings and elytra present in our species.....**Labidurinae.**

Subfamily PSALINAE

KEY TO THE GENERA AND SPECIES FOUND IN HAWAII

1. First antennal segment about as long, or as long, as distance between antennal sockets; excluding caudal tergite, all other tergites densely clothed with short, prostrate, conspicuous hairs borne from very dense, subconfluent punctures, tergites obviously dull under magnification.....**Anisolabis perkinsi** Burr.
- First antennal segment distinctly shorter than distance between antennae; the above-mentioned tergites shiny or comparatively so and with short, inconspicuous hairs..... 2
2. Femora all yellow, without a fuscous spot or ring about middle; length, excluding forceps, 15-16 mm.; forceps over 4 mm. long.....**Anisolabis eteronoma** Borelli.
- Femora usually with a fuscous spot or band about middle; length, excluding forceps, not over 14 mm., usually much smaller; forceps less than 3 mm. long.....**Euborellia annulipes** (Lucas).

Note: these species are extremely variable and considerable difficulty may be had in identifying some individuals. *A. perkinsi* and *A. eteronoma* are larger and have longer forceps than *E. annulipes*.

Genus ANISOLABIS Fieber, 1853

Anisolabis eteronoma Borelli (fig. 114).

Anisolabis eteronoma Borelli, 1909:315.

Anisolabis littorea (White) of Bormans, 1882:339; not *Forficula littorea* White, 1874.



Figure 114—Some earwigs. From left to right, *Anisolabis eteronoma* Borelli; *Euborellia annulipes* (Lucas); *Prolabia arachidis* (Yersin); *Sparattina nigrorufa* (Burr). (Not to same scale.)

Misnamed *Anisolabis maritima* (Géné) and *Anisolabis pacifica* Erichson in some Hawaiian literature.

Hebard, 1922:309, notes and discussion.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii (type from Hilo), Gardner Pinnacles, Pearl and Hermes Reef, French Frigate Shoal, Laysan.

Immigrant, but source undetermined. First recorded from the Hawaiian Islands by Bormans in 1882.

Habit: widespread; common in vegetable trash, rotten logs, rotting banana stems, under bark, under stones, in the soil and in similar situations in both the lowlands and mountains.

***Anisolabis perkinsi* Burr (fig. 115, a).**

Anisolabis perkinsi Burr, 1910:178.

Anisolabis xenia Kirby, misidentification by Burr, 1911:448; also evidently called *Anisolabis pacifica* Erichson in some Hawaiian literature.

Hebard, 1922:310, descriptive notes, pl. 26, figs. 1 and 2.

Kauai (type locality), Oahu, Maui, Hawaii.

Immigrant, but source unknown.

Evidently a mountain species. The dense hairs of the abdomen serve to distinguish it from *A. eteronoma*, but it appears to be very closely allied to that species.

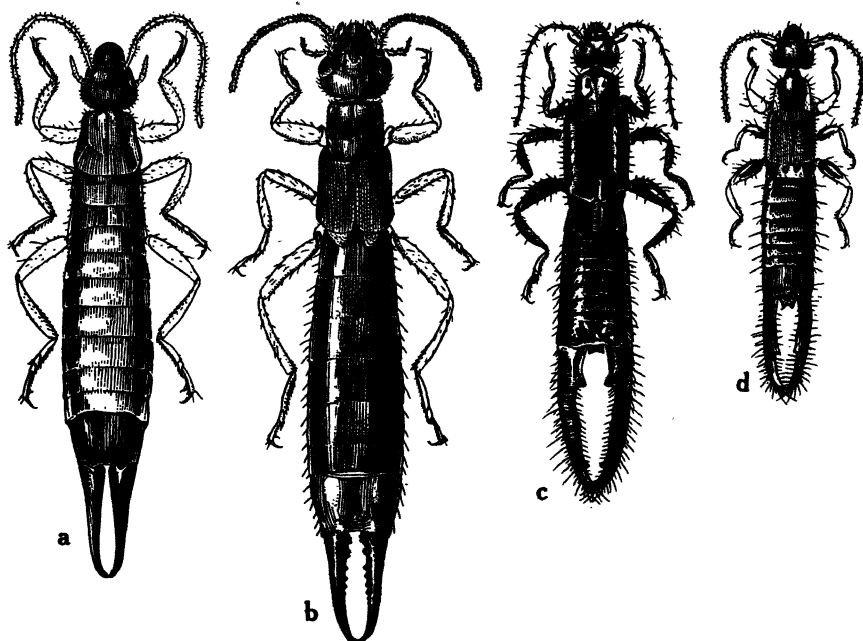


Figure 115—Some earwigs. **a**, *Anisolabis perkinsi* Burr; **b**, *Labidura riparia* (Pallas); **c**, *Sphingolabis hawaiiensis* (Bormans); **d**, *Labia dubronyi* Hebard. (Abernathy drawings; **a** and **b** to same scale, **c** and **d** to different scales.)

Some of Blackburn's early collections (about 1880 ?) are labeled *Anisolabis littorea*. One of Blackburn's female examples is 28 mm. long including the forceps.

Genus **EUBORELLIA** Burr, 1910

Borellia Burr, 1909.

The generic differences between this genus and *Anisolabis* are certainly not very obvious. The genus is said to be based upon characters found in the male genitalia.

Euborellia annulipes (Lucas) (figs. 114; 117, c-d).

Forficesila annulipes Lucas, 1847 :lxxxiv (type from Paris).

Anisolabis aporonoma Borelli, 1909 :317 (type from Honolulu).

The synonymy of this species is extensive; see Burr, 1910 :84, fig. 24.

The spotted- or ring-legged earwig.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii, Nihoa, Necker, French Frigate Shoal, Pearl and Hermes Reef, Midway.

Immigrant. Almost cosmopolitan. First recorded from the Hawaiian Islands by Borelli in 1909, but here earlier.

This is one of the commonest, if not the commonest, species of earwig in Hawaii and is widespread in the lowlands and uplands. It is extremely variable. Although it is normally without wings or elytra, a rare individual is occasionally discovered which has the elytra developed. Some specimens have the dark femoral bands obsolete. Although omnivorous, it was recorded as feeding almost exclusively on the sugarcane leafhopper during the early years of heavy damage by that pest. The eggs are laid under stones and trash, and the earwig may be found hiding during the day at the bases of leaves of sugarcane and *Freycinetia*, in trash and similar places. It carries the larvae of the poultry nematode *Subulura brumpti* (Alicata, 1939). Terry (1905:165) has published some anatomical notes.

Some specimens in Perkins' collection at the Bishop Museum are labeled as being very numerous in cases of Fijian plants inspected at Honolulu.

Subfamily LABIDURINAE

Genus LABIDURA Leach, 1815

Labidura riparia (Pallas) (fig. 115, b).

Forficula riparia Pallas, 1773:727.

Forficesila icterica Serville, Histoire Naturelle des Insects Orthoptères, Suites à Buffon, Paris, 1839:25 (I have not checked this reference).

For a detailed discussion and an introduction to the extensive and involved synonymy, see Burr, 1910:99-102, figs. 33, 34. Genotype of *Labidura*.

Kauai, Oahu, Molokai, Maui.

Immigrant. Cosmopolitan. First noted on Oahu soon after 1900.

This is our largest earwig; some specimens are about 30 mm. long, including the forceps.

Found beneath trash, under stones and similar places from the lowlands to at least 4,000 feet.

Family LABIIDAE Burr, 1909

Subfamily LABIINAE

KEY TO THE GENERA FOUND IN HAWAII

1. Wings wanting or aborted; pronotum and elytra without conspicuous discal hairs or setae; fifth antennal segment more than one-half as broad as long..... **Prolabia** Burr.
- Wings developed; pronotum and elytra either with sparse but distinct, long, erect hairs or dense short, conspicuous prostrate hairs over all; fifth antennal segment less than one-half as broad as long..... 2

2. Hair on pronotum, elytra and exposed parts of wings dense, conspicuous, prostrate or subprostrate, partially obscuring derm which, because of dense hair-bearing punctures, is dull **Labia** Leach.
 Hair on pronotum, elytra and exposed parts of wings sparse, widely spaced, long and erect, leaving derm fully exposed and shiny **Sphingolabis** Bormans.

Genus **PROLABIA** Burr, 1911

Prolabia arachidis (Yersin) (fig. 114).

Forficula arachidis Yersin, 1860:509, pl. 10, figs. 33-35.

See Burr, 1910:123, for detailed synonymy and fig. 82.

Oahu.

Immigrant. Cosmopolitan. First collected in Honolulu in 1914 by Swezey. There are few recorded captures of this species in Honolulu, and it is not certain that it is definitely established.

Genus **LABIA** Leach, 1815

KEY TO THE SPECIES FOUND IN HAWAII

1. Males 2
 Females 4
- 2(1). Forceps strongly arcuate, C-shaped, when closed leaving an almost O-shaped space between them **Labia curvicauda** (Motschulsky).
 Forceps not so shaped, straighter 3
- 3(2). Pygidium not visible when viewed from directly beneath (that is, not projecting beyond apex of last ventrite), its greatest expansion dorsal and nearly on same level as tops of forceps; wings extending beyond second visible tergite; pronotum broader than long **Labia pilicornis** (Motschulsky).
 Pygidium broadly and conspicuously exposed when viewed from beneath, its greatest expansion ventral and on a level beneath that of ventral faces of forceps; wings not or hardly projecting beyond first visible tergite; pronotum as long as broad **Labia dubronyi** Hebard.
- 4(1). Forceps with a dorsal and ventral row of teeth on inner sides **Labia dubronyi** Hebard.
 Forceps with at most a single row of minute denticles on inner sides 5
- 5(4). Pronotum about same color as elytra, dark brown, broader than long; inner surfaces of forceps vertical just behind pygidium and then dorso-laterally oblique (when closed distinctly separated just behind pygidium) **Labia pilicornis** (Motschulsky).

Pronotum distinctly yellowish and obviously paler than elytra to naked eye, fully as long as broad; inner surfaces of forceps conspicuously dorso-ventrally oblique from pygidium caudad (when closed their inner edges touch at base).....***Labia curvicauda*** (Motschulsky).

Labia curvicauda (Motschulsky) (fig. 116).

Forficesila curvicauda Motschulsky, 1863:2, pl. 2, fig. 1.

See Burr, 1910:118, for synonymy and fig. 38.

Kauai, Oahu.

Immigrant. Widespread in tropical and subtropical regions. First found by Swezey at Honolulu in 1915.

Labia dubronyi Hebard (fig. 115, d; 116).

Labia dubronyi Hebard, 1922:318, pl. 26, figs. 6-7.

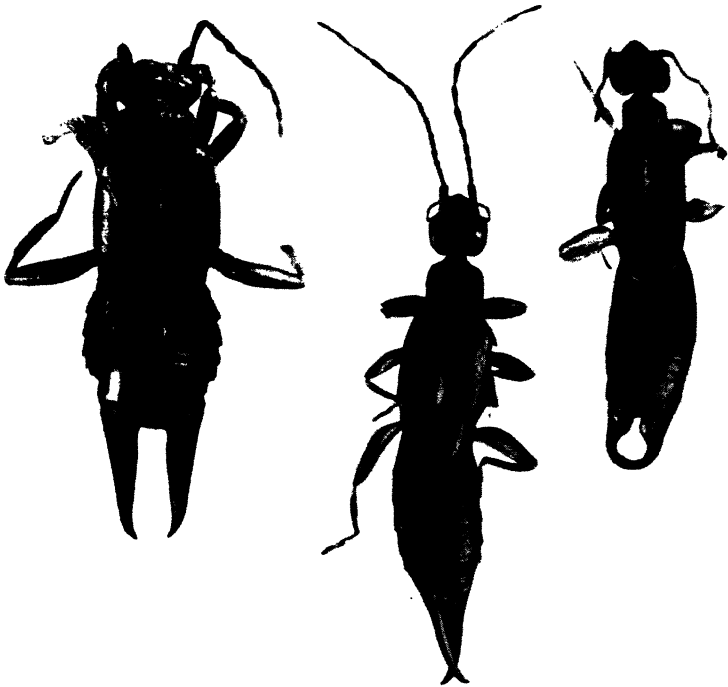


Figure 116—*Labia pilicornis* (Motschulsky), left; *Labia dubronyi* Hebard, center; *Labia curvicauda* (Motschulsky), right. (Not to same scale.)

Misidentified (?) by Bormans, 1882:340, 3 figs., as *Labia pygidiata* Dubrony, 1879.

Burr, 1910, pl. 5, fig. 41 (as *L. pygidiata*).

Labia swezeyi Hebard, 1932:31, fig. 1 (type from Mount Kaala, Oahu). New synonym.

Kauai, Oahu, Molokai, Maui, Hawaii (type from Hauula).

Immigrant. Known also from the Marquesas. First recorded by Bormans in 1882 from Oahu.

After examining a large series of individuals, I feel that *swezeyi* is based upon individual variants and is not a good species. The specimens at hand show a large amount of variation of the characters used by Hebard to separate his two "species." Hebard considers this species distinct from *Labia pygidiata* Dubrony with which other authors have associated Hawaiian specimens.

This species seems to be a forest insect only. It has been found under bark of various trees such as *Pisonia*, *Sideroxylon*, *Wikstroemia*, *Pipturus*, *Aleurites moluccana*, in rotting *Charpentiera* and banana stems, in rotting *Alectryon* fruits, and in *Astelja* and *Lobelia*.

Labia pilicornis (Motschulsky) (fig. 116).

Forficula pilicornis Motschulsky, 1863:2.

Burr, 1910:120, fig. 40. Hebard, 1922:316, pl. 26, figs. 3, 4: redescription.

Oahu, Hawaii.

Immigrant. Widespread in the Indo-Pacific regions. First found on Oahu by Swezey in 1914.

Recorded from behind leaf sheaths of sugarcane and on avocado.

Genus **SPHINGOLABIS** Bormans, 1883

Sphingolabis hawaiiensis (Bormans) (fig. 115, c).

Forficula hawaiiensis Bormans, 1882:341, 3 figs.

Kauai, Oahu, Hawaii (type locality).

Immigrant. Widespread in the Pacific from Malaya eastward. Described from Hawaii.

This is the largest (about 10–20 mm. long including the forceps) and apparently the most common member of the Labiidae found in Hawaii, but little is known regarding its habits here. It may be found in rotten banana stems and similar situations. It rather closely resembles *Chelisoches morio* and might be confused with that species. However, in addition to the differences between the tarsi, this species can be distinguished offhand because it has conspicuously hairy forceps whereas those of *Chelisoches morio* are bare.

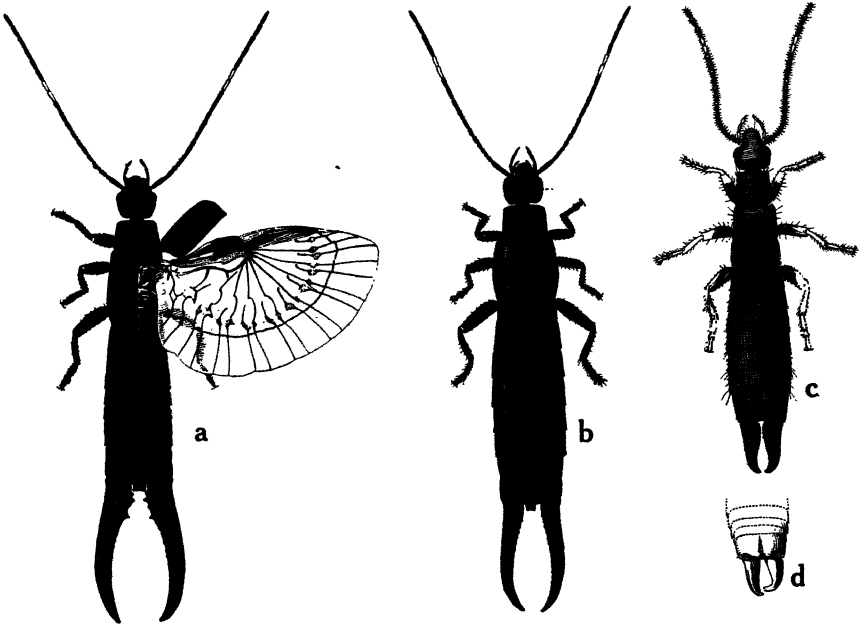


Figure 117—Two species of earwigs: **a, b**, male and female *Chelisoches morio* (Fabricius); **c**, *Euborellia annulipes* (Lucas), female, and apex of male abdomen at **d**. (From the original drawings for Terry, 1905.)

Family CHELISOCHIDAE Burr, 1907

Subfamily CHELISOCHINAE

KEY TO THE GENERA AND SPECIES FOUND IN HAWAII

1. Forceps shiny black, with at most a few hairs near their bases; pronotum, elytra and exposed parts of wings without hair (do not confuse the scattered marginal setae with hair); femora and tibiae shiny black . . . **Chelisoches morio** (Fabricius).
2. Forceps yellow, conspicuously clothed with long, fine hair from base to apex; pronotum, elytra and exposed parts of wings entirely and densely clothed with conspicuous hair; legs yellow . . . **Sparattina nigrorufa** (Burr).

Genus **CHELISOCHES** Scudder, 1876

Lobophora Serville, 1838, preoccupied.

Chelisoches morio (Fabricius) (figs. 117, a-b; 118, a-f; 119, A-B).

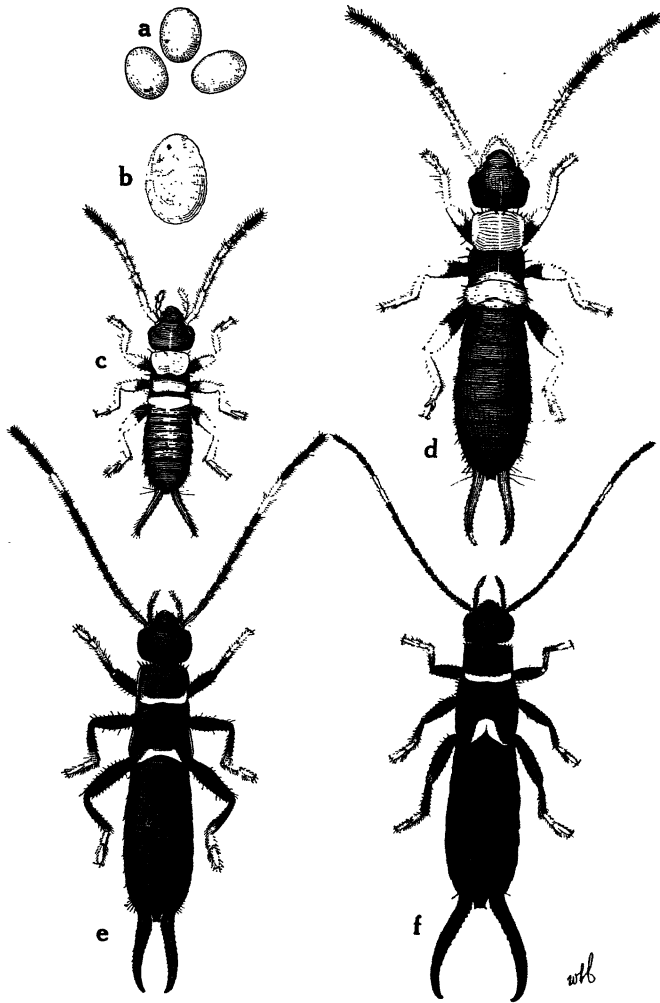


Figure 118—*Chelisochoes morio* (Fabricius), immature stages: a, eggs; b, embryo in ovum; c, first instar nymph; d, second instar; e, third instar; f, fourth instar. (From the original drawings for Terry, 1905.)

Forficula morio Fabricius, 1775:270.

For extensive synonymy see Burr, 1910:135, and figure. Genotype of *Chelisoches*.

The black earwig.

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii.

Immigrant. This Oriental species has been spread over most of the world by commerce. It is widespread on most of the high Polynesian islands. It was first found in the islands by some of the early voyagers to Hawaii.

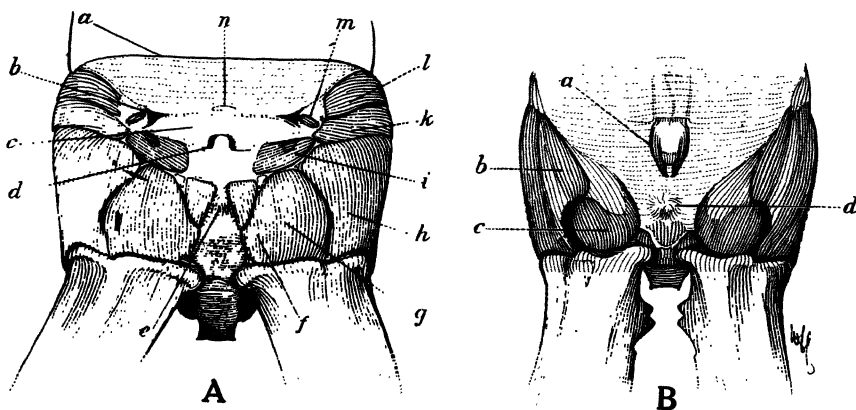


Figure 119—Details of genitalia of *Chelisoches morio* (Fabricius). A, Underside of apex of abdomen of female with seventh sternite removed to expose parts: a, cut edge of seventh sternite; b, sclerotized anterior angle of eighth sternite; c, membranous area representing eighth sternite; d, posterior chitinized emargination of eighth sternite; e, anus; f, articular part of tenth sternite (the articulation allows for the free passage of the feces); g, h, tenth sternite; i, thin sclerotized plate of ninth sternite; j, omitted by artist; k, ninth sternite; l, eighth sternite; m, seventh abdominal spiracle; n, genital opening. B, Underside of apex of abdomen of male with ninth sternite removed to expose parts: a, aedeagus; b, c, tenth tergite; d, anus. (From original drawings for Terry, 1905.)

This is one of the commonest earwigs found in Hawaii. It is readily recognized by its large size (up to more than 20 mm. including the forceps), shiny black derm and by the two pale antennal segments which are conspicuous in the living insect. It is common at the bases of leaves of such plants as *Cordyline* ("ti"), *Canna*, *Freyinetia* ("ieie"), *Dracaena* and sugarcane. Perkins (1913:ccxii) says that he saw it feeding on caterpillars and sugarcane leafhoppers and that "They often seize and hold their prey in their forceps." Perkins also recorded that the species fed upon the fruits of *Freyinetia* in the mountains. Terry (1905:164-171) prepared a detailed and excellent report on its anatomy, development and life history. He says:

It is an extremely active species, especially during the larval period, and appears to be diurnal, running over the leaves in search of insect food during the hottest part of the day. The adults will readily take to flight, the unfolding of the wings being a very rapid process and quite independent of the forceps, the writer never having seen them used either to assist in the folding or unfolding process. Wet localities seem to suit it best, since it abounds in the moist mountain ridges and valleys, and also in many of the elevated and wetter plantations. It is scarce in the dry and irrigated cane areas. Its predatory habits on leaf-hoppers have been observed by several people. Young hoppers are seized and devoured without the aid of the forceps, but these organs frequently assist in holding an adult hopper whilst it is eaten at leisure. An examination of numerous crops invariably revealed only insect remains, often entirely leaf-hopper. Those bred in captivity showed during all instars a marked preference for insect diet.

The eggs are deposited in a heap usually in the leaf sheaths of various large-leaved succulent plants such as *Canna* and sugar-cane, and are placed sufficiently far down to afford ample protection from the sun or enemies, the mother keeping continuous guard during the incubation period and for several days after the hatching of the young. She is most assiduous in her attentions to her ova, removing them carefully with the mandibles and palpi and constantly rearranging the batch...not infrequently however if disturbed, she will devour the entire lot. These batches consist of from about 40 to 60 eggs, the average number being about 45. Upon deposition they are of an ivory whiteness and broadly oval, measuring about 1 mm. $\times$ 0.75 mm.

There are five molts after hatching and the insect reaches adulthood in its sixth instar. The following data are derived from Terry's work: eggs hatch in 6 days, first molt on 12th day, second molt on 23rd day, third molt on 36th day, fourth molt and adult on 56th day. The number of generations in a year has not been ascertained. Terry (1906) also wrote an account of the development of the antennal segments of this species.

Genus SPARATTINA Verhoeff, 1902

Sparattina nigrorufa (Burr) (fig. 114).

Spongiphora nigrorufa Burr, 1902:4, pl. 20, fig. 3.

Hamaxas nigrorufa (Burr) Burr, 1915:118. Borelli, 1928:7.

Sparattina nigrorufa (Burr) Hebard, 1922:323, pl. 26, figs. 8, 9.

Hawaii.

Immigrant. Widespread in the Pacific. The earliest record I have of this species in Hawaii is from two male examples collected by Perkins at Hilo, Hawaii, in June, 1903, and from a single female taken by Blackburn on Hawaii (a note on this specimen written by Perkins says that it was taken about 1880). These three examples are in Perkins' collection at the Bishop Museum and their identity was unknown to Perkins.

This species has been found only on the island of Hawaii and nothing is known of its habits.

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Order ZORAPTERA Silvestri, 1913

(*zoros*, pure; *aptera*, wingless)

Zorapterans

Body soft; head large, fully exposed, hypognathous, trophi orthopteroid; mandibles large, dentate, masticatory; maxillary palpi five-segmented; labial palpi three-segmented; antennae longer than the head and prothorax, moniliform or filiform, nine-segmented (eight-segmented in nymphs); compound eyes and three ocelli present in winged forms or nymphs of winged forms, absent or obsolete in wingless forms. Thorax with the metathorax smallest, mesothorax intermediate, and prothorax largest; legs simple, cursorial; tarsi two-segmented, first segment much smaller than second; wings present or absent, slender when present, fore pair largest, folded back along abdomen at rest, bases petiolate, deciduous, venation greatly reduced, cross-veins few or absent, only one longitudinal vein in hind wing. Abdomen 10-segmented, the two caudal segments reduced; cerci present, not segmented; ovipositor absent; male with ninth ventrite absent, genitalia either symmetrical or asymmetrical. Metamorphosis simple; eggs laid free; small nocturnal insects, fungivorous or scavengers on dead arthropods (or carnivorous?), living in colonies beneath dead bark or in dead wood.

This small order contains a single genus of about 20 species. None has been found fossil. The described species are known from both North and South America, Africa and the Indo-Pacific regions; the group is predominantly a tropical and subtropical one.

Some workers consider the Zoraptera to be a suborder of the Corrodentia, but there appears sufficient reason for considering the group distinct. There are a number of morphological features which are similar to those of the Orthoptera and others suggestive of the Isoptera, but, on the whole, the structure of the Zoraptera is probably somewhat more like that of the Corrodentia than of any other order. However, it appears that the group is about equally representative of the orthopteroid series. Tillyard (1926) thought that it formed a connecting link between the Isoptera and the Corrodentia. When the order was first described, only the apterous forms were known, and Silvestri (1913) assigned them to the Apterygota.

The shedding of the wings is an interesting phenomenon shared with the termites. Although there is not such a distinct "fracture suture" at the wing bases as in the termites, the wings are shed by being broken off along a definite zone of weakness. Dealated individuals retain the stumps of their wings as do dealated Isoptera. The wings are shed within a few days after maturity is reached, according to Gurney (1938).

A low type of caste system is suggested by the two forms of reproductives. One group attains sexual maturity without developing wings, whereas the other "caste" possesses wings at maturity. The winged forms are darkly pigmented, have the eyes and ocelli fully formed and develop from nymphs which usually have the compound eyes and ocelli present but feebly developed. The apterous forms are not pigmented, or at most are weakly pigmented, lack ocelli and have the compound eyes absent or at most feebly developed. The later stage nymphs of the winged forms have distinct wing pads which are never produced in the apterous forms. The number of instars has not been ascertained. The apterous forms are more numerous than the alates.

Zorapterans are usually found in colonies, and some writers have considered them subsocial. However, it is probable that they are only gregarious.

A specimen of *Zorotypus swezeyi* examined by me appeared to have the alimentary canal full of finely divided plant material (moldy wood?). No records of parasites of this order have come to my attention.

Family ZOROTYPIDAE Silvestri, 1913

Genus ZOROTYPUS Silvestri, 1913

Zorotypus swezeyi Caudell.

Zorotypus swezeyi Caudell, 1922:133. Gurney, 1938:72, pl. 3, figs. 42-43.

Kauai (type locality: Kokee), Oahu.

Immigrant(?). Caudell thought that this was a foreign species, perhaps "East Indian."

It appears to be a rare insect. A few specimens have been collected from rotten logs of *Acacia koa* on Kauai and Oahu, a rotten *Straussia* log on Oahu, and a rotten *Metrosideros* stump on Oahu. Only a single winged specimen has been found, and all the other examples collected have been apterous forms. All individuals taken have been collected exclusively in the damp mountains. The first specimens were found on Kauai in August, 1921, by Dr. Swezey.

Because the material now available is not adequate for illustration, I have reproduced Gurney's figures (1939) of the Fijian *Zorotypus zimmermani* Gurney, to illustrate the group. The female of this Fijian species is not greatly unlike that of the Hawaiian insect.

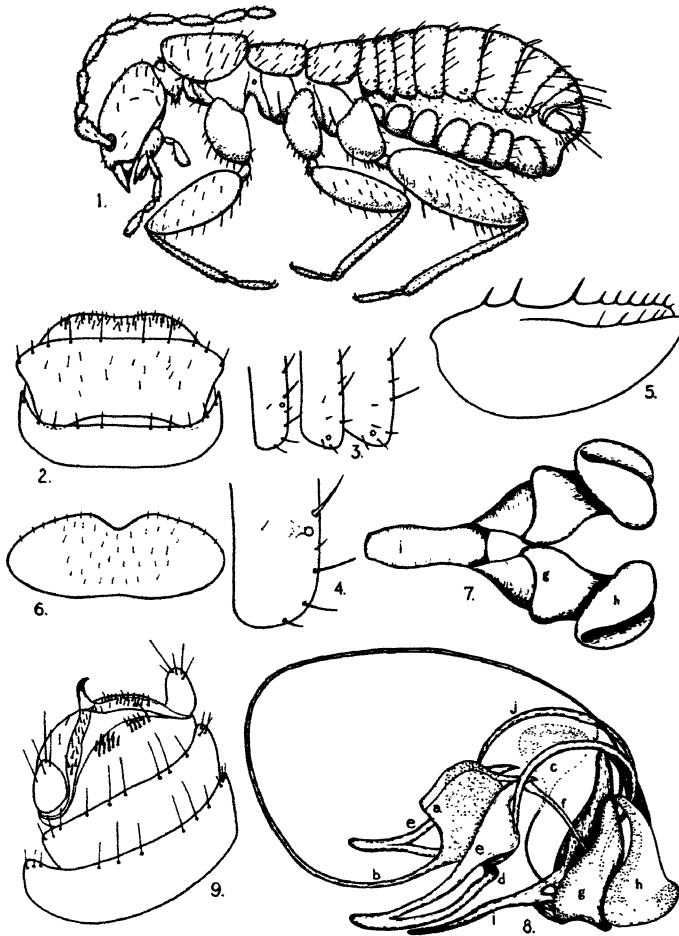


Figure 120—*Zorotypus simmermani* Gurney. Although this Fijian species does not occur in Hawaii, this figure is reproduced here because adequate material of the Hawaiian form is not available. This species closely resembles the Hawaiian species, and the plate gives a good outline of the features of the order. 1, Apterous female; 2, subgenital and adjoining plates of apterous male; 3, left lateral part of tergites 1 to 3 of apterous female; 4, left lateral part of first tergite of apterous female; 5, outline of hind femur of apterous male, lateral view; 6, ventral view of subgenital plate of apterous female; 7, paired lobes and basal plate of genitalia of apterous male; 8, dorso-lateral view of genitalia of apterous male; 9, dorso-caudo-lateral view of apex of abdomen of apterous male. (After Gurney, 1939.)

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Order **CORRODENTIA** (Burmeister, 1838)

(*corrodens*, gnawing)

Copeognatha Enderlein, 1903.

Psocoptera Shipley, 1904.

Psocids, Barklice, Booklice

Body comparatively soft, usually in part subject to shrivelling after death; head hypognathous or prognathous, large, exposed, free; labrum well developed; both anteclypeus (clypeolus) and postclypeus (clypeus; usually conspicuously inflated and bulbose) present; epicranium divided by a longitudinal median suture and joining a V-shaped suture separating the front and vertex; mandibles masticatory, asymmetrical, dentate, the teeth of one mandible fitting into grooves between the teeth of the other, molar area present; maxillary palpi four-segmented; labial palpi one- or two-segmented; maxillae bearing a pair of peculiar, long, retractile, chisel-like sclerotized rods (modified laciniae) ensheathed by the galea and capable of extrusion for a considerable distance from the "mouth" (rarely, these organs are absent); antennae elongate, filiform, 13- to about 50-segmented, longer than the body in most of our species; compound eyes (excepting in a few forms) large and in many species strongly protuberant, widely separated; ocelli present or absent (present in the majority of forms), three in number, the anterior one on the frons, the posterior pair lying one on either side of the median suture of the epicranium. Thorax with the prothorax large in some forms, but greatly reduced and largely concealed in most of the winged groups; mesothorax larger than metathorax. Legs usually cursorial, rarely saltatorial, tarsi two- or three-segmented, claws paired, empodium present. Wings variable, absent, partially or unequally developed or with four functional wings usually held roof-like over the body (but held flat over the body in some species when at rest), fore pair larger and with more complex venation than hind pair, true cross-veins absent or at most one or two present, a pterostigma present in fore wings of many forms, venation characteristic and comparatively simple, as in figure 121. Abdomen 10-segmented, the first sternite reduced or obsolete, the two terminal segments reduced; cerci absent; ovipositor present or absent; male genitalia symmetrical or asymmetrical, comparatively complicated in form and structure in many groups. Metamorphosis slight; eggs plain or sculptured, deposited singly or in groups on foliage, bark or other substratum in the vicinity of the food source, concealed by some forms beneath webs, enclosed in groups under a cement-like or dried frothy or crusty material (an anal secretion) in other forms, laid bare in others; some species viviparous, others parthenogenetic, but mostly normal in development; six instars, wing

buds present in second instar; mostly diurnal; mostly fungivorous, algivorous or lichenivorous, but with a varied assortment of habits within the order (some wingless forms have been recorded from living mammals), although the group is predominantly herbivorous (Pearman found that algae of the genus *Pleurococcus* formed the principal food of some psocids, and that certain psocid species ate only particular species of *Pleurococcus*); some species live in small colonies beneath delicate webbings and most are rapid in their movements. Pearman (1932: 90-96, figs. 1-8), gives notes and descriptions of coccophagous species which were said to feed upon *Pseudococcus citri* in East Africa.

Fossil psocids have been described from the Miocene, Oligocene and Upper and Lower Permian. The Permian species had five-segmented tarsi—the primitive hexapod tarsal number. There are evidently about 1,000 living species known today, but further study will greatly expand this number.

There are 40 species listed here as occurring in Hawaii, but I have seen several additional unrecorded species. Of the total number of recorded species, 24 are endemic, whereas the other 16 are all considered immigrants. The native forms belong to the genera *Psocus*, *Kilauella* and its offshoot *Palistreptus*. They are Polynesian derivatives.

Many psocids spin silk from the openings of their silk glands in their oral cavities to use in covering their eggs or to produce a webbing beneath which they live in small colonies. Some extra-Hawaiian species spin large amounts of webbing on trees and thus produce an unsightly appearance. It is thought that the webbing serves as an efficient protection from enemies—especially ants.

Psocids have many enemies. The minute mymarid wasp *Alaptus* parasitizes the eggs of some species. Ants, green and brown lacewings, dolichopodid flies, emesid and reduviid bugs are known to prey upon them. They probably constituted the principal food for such predators as the lacewings in these originally aphid-free islands.

Many species are rapid in movement, and many, although fully capable of active flight, will show great reluctance to take wing and will dodge about on their host-plants even if persistently annoyed and pursued.

The Corrodentia are evidently most closely allied to the Zoraptera which connect them with the orthopteroid stocks on the one hand, and to the lice—the Mallophaga and Anoplura—on the other hand. Tillyard (1923:173) believed that the lice were derived from an ancient wingless psocid stock, and he points out that "...it is worthy of note that wingless Psocoptera are even known at the present day to live upon mammals." Weber (1939, reference not seen) placed the Mallophaga, Anoplura and psocids all in one group, the Psocoidea.

The usual wing venation in the Corrodentia is quite distinct from that found in any other order of insects. Figure 121 and others adequately illustrate the usual types of venation. The absence of true cross-veins is striking. The irregular courses of sections of the main veins replace cross-veins. The only insects which have wing venation which superficially resembles that of the Corrodentia are the Psyllidae and Coniopterygidae—unrelated groups—and the allied Zoraptera.

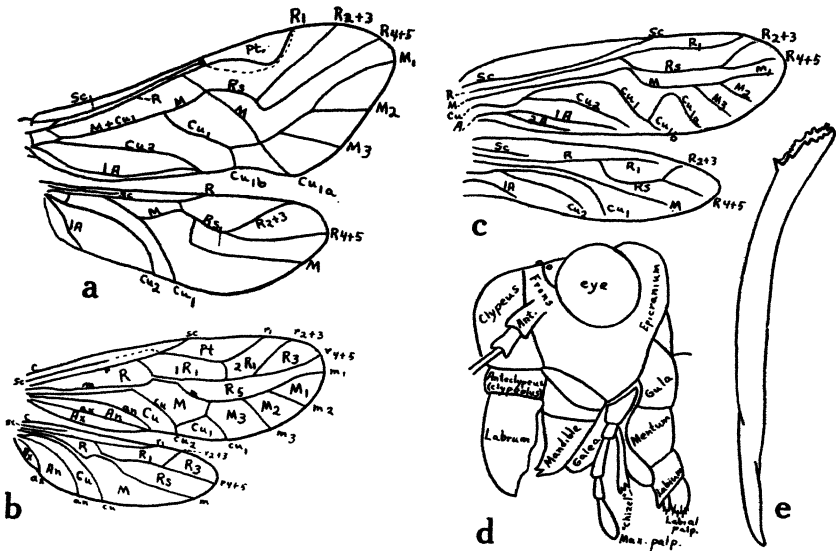


Figure 121—Details of psocids: a, wings of *Myopsocus* (redrawn from Tillyard, 1923); b, wings of *Caecilius* (veins drawn separated to show courses), veins labeled in lower case letters, cells in capital letters (redrawn from Enderlein, 1903). (Note the difference in nomenclature used by Tillyard and Enderlein.) c, Tracheation of wings of last nymphal instar of a *Psocus* (redrawn from Tillyard, 1923); d, head of a *Psocus* (redrawn from Enderlein, 1903); e, maxillary "chisel" (redrawn from Enderlein, 1903).

The peculiar maxillary chisels ("maxillary forks," "picks," "styliform appendages," "laciniae," "rods," "paragnatha," "furcae maxillares") are unique among insects. However, a rather similar structure is said to be found in certain Mallophaga. It is thought by some workers that these structures are used to cut fungal mycelia and other food and for bursting fungal spore cases; but Pearman (1928: 268) does not agree that they are used for such purposes. These organs are usually complexly dentate or incised at the apex and afford good characters of identification.

The psocids found in Hawaii range in size from about 1 mm. in length in the wingless immigrant *Liposcelis* to slightly more than 1 cm. in wing expanse in certain endemic *Psocus*.

The Corrodentia are a taxonomically difficult assemblage, and great differences of opinion as to their classification exist among various authors who have studied them. Comstock, in his *An Introduction to Entomology* (1933), recognized only two families in the order, but Pearman's classification of 1936 lists 26 families in eight supra family categories. In 1909, Enderlein divided the order into two sub-orders principally on the basis of the number of segments in the tarsi. According to this view, the suborder Isotecnomena contains those psocids whose immature and mature stages have two-segmented tarsi, and the single-segmented labial palpi.

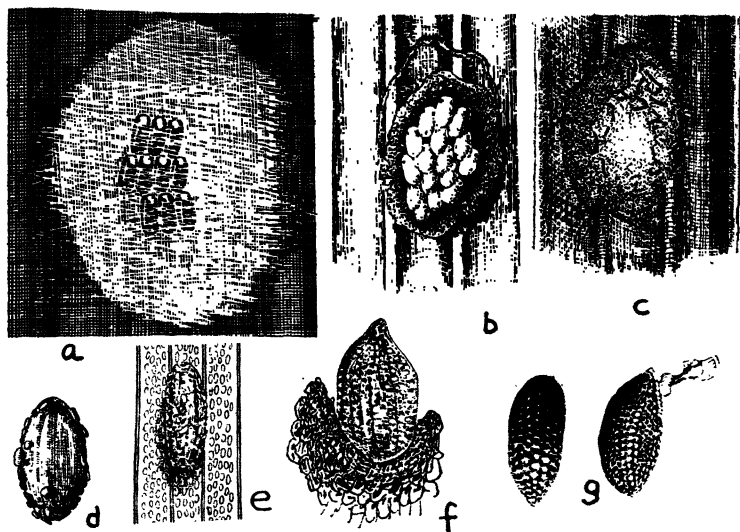


Figure 122—Eggs of some psocids: **a**, *Caccilius analis* Banks, webbed-over cluster of eggs on leaf of sugarcane, eggs 0.5 mm. long; **b-c**, uncovered and covered cluster of eggs of *Hemipsocus roseus* (Hagen) on a sugarcane leaf, cover about 3 mm. long; **d**, egg of *Ectopsocus fullawayi* Enderlein, length about 0.35 mm.; **e**, egg of *Psylloneura williamsi* Banks, on leaf of sugarcane, length about 0.45 mm.; **f**, egg of *Cyrtophania hirsuta* Banks, length about 0.45 mm.; **g**, eggs of *Lepidopsocus costalis* (Banks), right egg hatched and showing cast amniotic membrane, egg length 0.4–0.5 mm. (Rearranged from Banks, 1931.)

The suborder Heterotectnomera contains psocids whose immature stages have two-segmented tarsi, but the adults have three-segmented tarsi and most of them have two-segmented labial palpi. Tillyard (1923:173), commenting upon this classification, said, "... it seems quite clear that this subdivision does not represent the original dichotomy of the order, but merely separates the three most highly specialized families from all the rest. The more archaic representatives of the order are so rare, and so little is known about them that much more work remains to be done before we shall be in a position to offer a classification of the order which truly represents its main lines of evolution." In 1926, Tillyard, after studying fossil psocids, proposed a new division of the order based upon wing venation, antennal and prothoracic characters and used the subordinal names Parapsocida and Euopsocida. It seems to me that Tillyard's work warrants more credit and consideration than it appears to have received. Banks, in 1929, proposed a different and much simplified classification of the order based principally on wing venation. Karny (1930) published a detailed revised classification with keys to families, subfamilies and tribes and a complete list of the genera. Karny's system is quite different from any of the others. Pearman (1936) has proposed a radically revised classification, but, unfortunately, his published work includes only an outline unsupported by descriptive details. He is, however, preparing a detailed and com-

prehensive revision of the order, but owing to the difficulty of the task, it will be a long time before his results will be available in published form. Each of the above-mentioned systems differs greatly from the others, and to one unfamiliar with the group it appears that psocid taxonomy is in chaos.

For these and other reasons, it is felt that this work would better serve the Hawaiian students if a simpler and more or less arbitrary and tentative classification were used. Thus, the conclusion has been reached that a compromise arrangement is the more feasible course to follow for the Hawaiian species at the present time. It is one of the principal aims of this volume to aid students in determining their material, and an arrangement of the psocids is presented here which, it is hoped, will aid the worker more than if an attempt were made to follow entirely any one authority. However, the original manuscript has been revised to make it fall more in line with Pearman's work. The keys and general classification used here are not intended to be natural arrangements—the text is written principally to facilitate identification. In all the keys in this chapter, the characters used are based principally upon Hawaiian psocids, and it is not intended that they will hold good for other faunas. It must remain for some future worker to place the Hawaiian Corrodentia upon a sound and proper foundation.

[*Note.* After this manuscript was completed, Mr. Pearman sent me a carefully and laboriously prepared outline of his revised classification, complete with meticulously drafted illustrations. With utmost generosity he suggested that I incorporate his entire work in this manual. I appreciate greatly his unfettered spirit of scientific cooperation, but I feel that the revolutionary results of his long labors should await the time when they can be published entirely under his own name with the full and just credit falling where it should. If it had not been for the war and the consequent delays of communication and other resultant impediments, we might have worked out the Hawaiian psocids in closer cooperation. I owe Mr. Pearman many thanks for answers to numerous questions and other aid given in spite of the handicaps of wartime conditions in war-torn England. It is to be hoped that he may complete without further delay his revised classification with ample keys, descriptions and illustrations and have them published so that they may be available to all workers.]

The Corrodentia of Oceania are poorly and inadequately known. Future studies of collections assembled at the Bishop Museum and elsewhere will probably reveal that a number of the immigrant species which are now known only from the Hawaiian Islands are widespread on other Pacific islands. A cursory examination of some of our collections has already revealed extra-Hawaiian distribution for some species (for example, see *Ectopsochus*). The Hawaiian psocids have received more attention than those of any other Polynesian archipelago, but only three men—Perkins, Enderlein and Banks—have studied our species systematically, and much remains to be done. Perhaps not one-half of our local psocid fauna is known.

This group offers a fertile field of endeavor for a careful, ambitious worker. Most species shrivel considerably upon drying, and, without considerable care,

many psocids mounted dry are difficult to work with. For this reason, perhaps, few workers are encouraged to specialize in these interesting animals. Some workers prefer material collected and preserved in alcohol. However, the hairy and squamose species lose their wing scales and hairs and their colors are hard to distinguish in alcohol-preserved material. Excellently prepared specimens of at least the larger forms can be had if the individuals are carefully collected in dry vials and mounted with great care promptly after death. Dry material supplemented by duplicates preserved in alcohol or mounted on slides will greatly aid in the study.

TABULAR ANALYSIS OF THE HAWAIIAN CORRODENTIA

FAMILY	GENERA	ENDEMIC GENERA	NON- ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Perientomidae	2	0	2	4	0	4
Psoquillidae	1	0	1	1	0	1
Liposcelidae	1	0	1	1	0	1
Pachytroctidae	1	0	1	1	0	1
Psocathropidae	2	0	2	2	0	2
Caeciliidae	2	0	2	2	0	2
Peripsocidae	2	0	2	4	0	4
Hemipsocidae	1	0	1	1	0	1
Elipsocidae	2	2	0	10	10	0
Psocidae	1	0	1	14	14	0
Totals	15	2	13	40	24	16

Percentage of endemism in native group: genera 66% percent; species 100 percent.

Percentage of present-day fauna native: 60 percent.

Percentage of present-day fauna adventive: 40 percent.

Average number of species per genus in native group: 8.

Average number of species per genus in adventive group: 1.3.

KEY TO THE FAMILIES OF CORRODENTIA FOUND IN HAWAII

1. Wings absent; meso- and metathorax fused so that thorax appears to be only two-segmented; hind femora broadly expanded **Liposcelidae.**
At least fore wings present, although all wings may be reduced in size; thorax normal, three-segmented; hind femora not so expanded..... 2
- 2(1). Fore wing membrane densely hirsute or squamose..... **Perientomidae.**
Fore wing membrane not hirsute or squamose..... 3
- 3(2). Hind wings greatly reduced in size or absent..... 4
Hind wings present and at least moderately large..... 6
- 4(3). Tarsi two-segmented; ocelli present; wings as illustrated (fig. 127, e)..... *Chaetopsocus* of **Peripsocidae.**
Tarsi three-segmented; ocelli absent; wings obviously different 5
- 5(4). Fore wing with a cross-vein between R_1 and R_s , thus making a closed cell at about middle of wing, as illustrated (wings clear in our species) (fig. 127, c)..... *Psocathropus* of **Psocathropidae.**

- Fore wing without such a cross-vein and closed cell, as illustrated (wings opaque brown in our species) (fig. 126, c-d) **Psoquillidae**.
- 6(3). Fore wings without a distinct pterostigma (fig. 127, a-b) ... 7
 Fore wings with radius subsinuate distad and forming a distinct pterostigma (fig. 130) 8
- 7(6). Fore wing with a cross-vein between R_1 and R_s , thus making a distinct, closed cell at about middle of wing, as in figure 127, b. *Psyllipsocus* of **Psocathropidae**.
 Fore wing without such a cross-vein and closed cell.
 *Psylloneura* of **Pachytroctidae**.
- 8(6). Fore wing with areola postica (cubital cell) absent (figs. 127, e; 129) **Peripsocidae**.
 Fore wing with areola postica present (fig. 130) 9
- 9(8). Fore wing vein Cu_1 either touching or joined to vein M by a cross-vein so that enclosed cells M and M_s are formed (figs. 130, a; 135) 10
 Fore wing with vein Cu_1 distant from M and not forming cells M and M_s (fig. 130, b) 11
- 10(9). Fore wing veins without setae **Psocidae**.
 Fore wing veins with setae 12
- 11(9). Tarsi two-segmented **Caeciliidae**.
 Tarsi three-segmented (check carefully; the second segment is difficult to see on some dried specimens; it may be necessary to put a tarsus in alcohol or other fluid to see the segments distinctly) **Elipsocidae**.
- 12(10). Tarsi two-segmented **Hemipsocidae**.
 Tarsi three-segmented part of **Elipsocidae**.

Family PERIENTOMIDAE Enderlein, 1927

The Hawaiian members of this family can be distinguished from all our other psocids because the fore wings are densely clothed with hairs and scale-like hairs. The tarsi are three-segmented. Pearman (1936) uses Lepidopsocidae for this group, but *Perientomus* is the older name.

KEY TO THE GENERA OF PERIENTOMIDAE FOUND IN HAWAII

1. Hind wings developed **Lepidopsocus** Enderlein.
2. Hind wings aborted **Cyptophania** Banks.

After examining drawings prepared by me, Mr. J. V. Pearman, in a letter dated February 14, 1940, states that *Echmepteryx marmorata* Banks really belongs to *Lepidopsocus*. The other local *Echmepteryx* follow this species into *Lepidopsocus*. The new combinations appear below.

Karny (1930) assigns both *Lepidopsocus* and *Echmepteryx* to the Echmepterygini of the Perientominae, which he includes with the Amphientomidae.

Genus **LEPIDOPSOCUS** Enderlein, 1903

This is an Indo-Pacific genus with representatives also on certain islands of the Indian Ocean. The wings are narrow and characteristically pointed at their apices.

KEY TO THE SPECIES FOUND IN HAWAII

1. Hind wings with vein R_{2+3} distinctly more than one-half as long as R_{4+5} , arising from R_2 at a point only about one-fourth of its length from origin of M_{1+2} (see fig. 124, c)..... **marmoratus** (Banks).
Hind wing with vein R_{2+3} distinctly less than one-half as long as R_{4+5} and arising from R_2 at a point distinctly more remote from origin of M_{1+2} than its length (see fig. 124, a-b)..... 2
2. Vestiture of fore wings dark brown from base to apex down median part of the wing, and with a band of white along both fore and hind margins; venation of hind wing as in figure 124, b; hair on head not very dense and shaggy..... **costalis** (Banks).
Vestiture of fore wings almost concolorous, golden or yellowish brown, without a distinct dark and pale pattern; venation of hind wing as in figure 124, a; head bristling with very dense, shaggy hair..... **unicolor** (Banks).

Lepidopsocus costalis (Banks), new combination (figs. 122, g; 123; 124, b).

Echmepteryx costalis Banks, 1931:439, pl. 7, fig. 3; pl. 8, fig. 3; pl. 9, fig. 4 (eggs).

Oahu (type locality: Ewa).

Immigrant, but source unknown.

This species has been found on sugarcane, coconut, papaya and other plants.

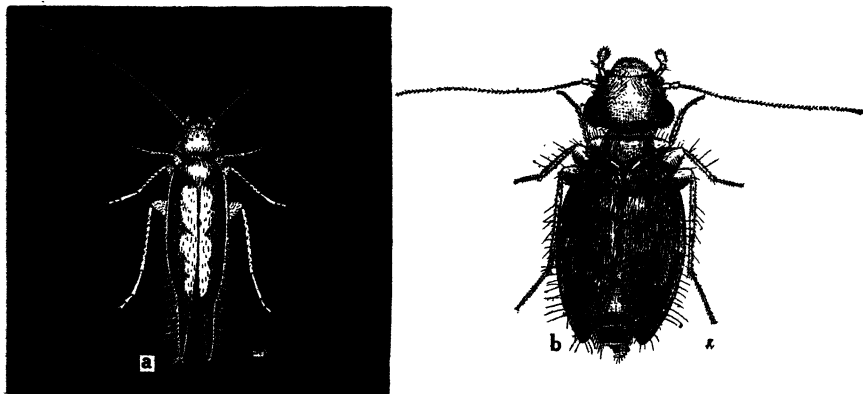


Figure 123—*Lepidopsocus costalis* (Banks), left; *Cyptophania hirsuta* Banks, right. (From original drawings by Yamamoto and Williams for Banks, 1931.)

The color pattern on fresh, unrubbed specimens is striking and diagnostic. The dark scales, some of which are iridescent, make a broad vitta down the entire length of the wing, and the fore and hind margins are white and contrast sharply.

Lepidopsocus marmoratus (Banks), new combination (fig. 124, c).

Echmepteryx marmorata Banks, 1931:439.

Oahu (type series from Kualoa and Honolulu), Maui.

Immigrant, but source unknown.

Hostplants: tomato, *Acacia koa*, *Albizia*, *Coprosma*, *Erythrina*, *Euphorbia*, *Plumeria*.

The fore wings are conspicuously spotted with white and brown.

Lepidopsocus unicolor (Banks), new combination (fig. 124, a).

Echmepteryx unicolor Banks, 1931:439.

Immigrant, but source unknown.

The golden or yellowish fore wings are distinctive.

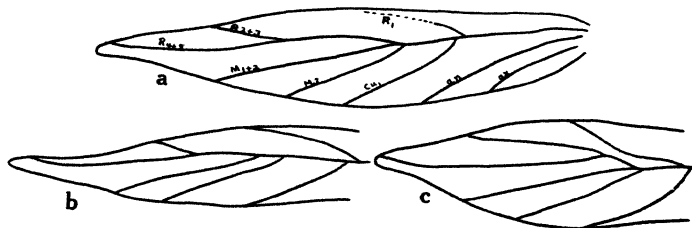


Figure 124—Sketches of hind wing venation of *Lepidopsocus* species: a, *L. unicolor* (Banks); b, *L. costalis* (Banks); c, *L. marmoratus* (Banks).

In addition to these three species, Swezey and I have each collected a specimen of a beautiful yellow-gold species which has as yet not been identified. It will run to *unicolor* in the key, but its color, wing venation and less densely hairy head will serve to distinguish it.

Genus **CYPTOPHANIA** Banks, 1931:440

Cryptophania (Banks), error in Neave, Nomenclator Zoologicus, 1939.

This genus is monotypic. The hind wings are wanting. Banks originally placed it as a relative of *Psocinella*.

Cryptophania hirsuta Banks (figs. 122, f; 123).

Cryptophania hirsuta Banks, 1931:440, pl. 7, fig. 1; pl. 8, fig. 7; pl. 8, fig. 5 (eggs).

Oahu (type locality: Honolulu), Hawaii.

Immigrant. Source unknown.

The type series was taken on sugarcane, and others have been taken on *Urera*, *Acacia koa*, *Sideroxylon* and on ferns, including *Cibotium*, in the mountains.

This peculiar, running and jumping species is easily recognized because of its densely hairy brown fore wings which are more or less elytra-like and fit together in a straight line for more than one-half of their lengths down the back and do not overlap. There are two types of hair on the wings: one is prostrate, whereas the other is long and bristling erect.

Williams (1931:88) says, "The eggs are somewhat like those of *Echmepteryx [costalis]*, but stouter and of a sort of salmon color. It occurs in the mountains, and in the cane fields is more or less terrestrial."

Family PSOQUILLIDAE Kolbe, 1884

Genus PSOQUILLA Hagen, 1865:123

Psoquilla margine-punctata Hagen (fig. 126. c-d).

Psoquilla margine-punctata Hagen, 1865:123. McLachlan, 1867:7, pl. 2, fig. 4.

Enderlein, 1925:107, fig.

Heteropsocus dispar Verrill, 1902:817, figs. 192, 192a-b (described from Bermuda).

Kauai, Oahu.

Immigrant. Widespread in the tropics; described from a specimen taken in a German hothouse. First found in Hawaii at Honolulu by Swezey in 1918.

This species is easily recognized among our psocids because of its distinctly spotted fore wings. The wing membrane is brown with conspicuous white spots arranged as in figure 126. Roesler (1940:225, fig. 1) discusses and figures the macropterous female; I have not seen the macropterous form in Hawaii. (See also Pearman, 1935:83-84.)

Dr. Swezey found this species in bran in Honolulu and on the bark of "kauwila" (*Alphitonia* ?) on Kauai. Takahashi (1938:11) said that this species has been found abundant in stored grain in Formosa. I found it common on moldy boards on the sides of boxes containing rotten fruits from which melon flies were being bred in June, 1943. It runs very rapidly and is difficult to capture.

Family LIPOSCELIDAE Pearman, 1936:59

Trogidae Enderlein, 1911.

Atropidae Kolbe, 1884 (*Atropos* is invalid; it is a synonym of *Trogium*. See Gurney, 1939:510).

Troctidae, of authors.

The fused meso- and metathorax together with the absence of even vestiges of wings will readily distinguish this family from the others found in Hawaii. The tarsi are three-segmented.

Genus **LIPOSCELIS** Motschulsky, 1853

There is more than one species in this genus established in Hawaii, but I have been unable to identify them.

Liposcelis divinatorius (Müller) (fig. 125).

Termes divinatorium Müller, 1776:184.

See Gurney (1939:513) for synonymy and discussion.

The booklouse (also called the death watch, cereal psocid, book-tick and cabinet mite).

Widespread in Hawaii and probably present on at least all the main islands, but no detailed locality records have been assembled.

Immigrant. Cosmopolitan. It has been in the islands for many years.

Parasite: *Alaptus globosicornis* Girault (Hymenoptera: Mymaridae, a minute insect, and one of the smallest of all insects in Hawaii, if not the smallest), in the eggs.

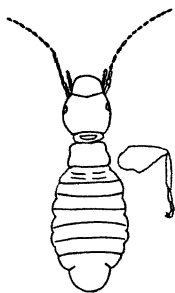


Figure 125—*Liposcelis divinatorius* (Müller) ?; the hind leg is separately outlined.

A widespread insect long associated with man. It is a common pest in warehouses, stores, kitchens, museums and other places where it attacks, especially, cereals and cereal products; it also damages insect, plant and other museum collections, and it has been accused of feeding upon various plant and animal materials as well as the pastes in book bindings. Large colonies are likely to develop on moldy articles, because certain fungi are eagerly consumed. In fact, it is probable that fungi usually constitute the principle diet of this psocid, but colonies will sustain themselves for years on dry cereals where no mold is present. In spite of its omnivorous habits, however, this pest is most important economically because of

its infesting foodstuffs—especially cereals. It is not so much the consumption of food materials that makes the insect a pest as its mere presence which causes much infested food to be thrown away. I have had many infestations in flour, yellow corn meal and ground breakfast cereals in my own kitchen and have seen examples taken from prepared fish food and almonds, and Mr. Pemberton has shown me polished rice and dried yeast which were considerably damaged by this insect. In spite of these and other similar observations, Back (1939:3) refers to them as "harmless creatures." The minute size of the insect gives it access to packaged articles which may appear to be insect-proof.

This insect has long been accused of damaging book bindings, paper and other materials, but the latest information available leads to a contrary conclusion. Back (1939) suggests that damage caused by cockroaches and silverfish has been erroneously assigned to psocids.

This species is only a millimeter or somewhat more in length, completely apterous, grayish white or pale yellowish with black eyes; the meso- and metathorax are so fused that the thorax appears to consist of only two segments; the eyes are unusually small; the hind femora are enlarged, as illustrated in figure 125. It is considered the smallest known psocid.

Back (1939:3) notes that in the southern United States in summer the "... eggs hatch in 4 to 11 days, and each female lays on an average of about 60 eggs" and that "Development from egg to adult may be completed in from 3 to 4 weeks during the warmer months." No life history studies have been made in Hawaii to my knowledge. This species develops parthenogenetically. Rosewall (1930) found no males after several years' study of laboratory cultures.

Pearman (1928:216) says, "Eggs scattered, ovoid, translucent greyish with purplish iridescence, more or less thickly sprinkled with granular particles derived from surrounding objects; no enveloping pellicle observable." *

These psocids are reported to require warmth and high humidity for optimum development and are especially apt to build up large populations during warm, damp weather. Evidently the conditions that favor the development of minute molds are largely responsible for the fluctuations of populations in Hawaii. Damp places such as basements usually support thriving colonies and damp wood and other damp articles are likely to be infested. On the other hand, I have kept a colony thriving for several years in a tightly closed jar of dry corn meal.

The term "death watch" comes from the alleged habit of these insects making a ticking sound by striking their venters against whatever they happen to be on, thus occasionally making a faint but audible sound. Imms (1934), following Pearman, says that sound production has not been proved for this species, but it has for "*Clothilla pulsatoria* and *Lepinotus inquilinus*," and that the ticking is considered a mating call employed by the female.

Control: The best control is fumigation with a fumigant such as hydrocyanic gas or methyl bromide. Carbon tetrachloride is good for eliminating infestations in insect boxes, cabinets and similar small enclosed articles and is safe to use in the

home. Naphthalene and paradichlorobenzene will prevent infestations and will kill out the pests if confined. A 5 percent solution of DDT sprayed over areas infested with psocids will give good control for a long time. Rooms and similar places can be cleared by heating to 125° F. for several hours. Infested foodstuffs may be carefully heated in an oven at 125° to 130° F. to destroy all stages. Infested moldy articles such as shoes and boots should be wiped clean, dusted and placed in direct sunlight for several hours to kill all stages. Pyrethrum, derris and sodium fluoride dusts and oil-pyrethrum sprays are effective in control. Although control methods may rid a place of these psocids, it is likely that reinfestation will occur in a short time because of the abundance and widespread distribution of the animals and the ease with which they gain access to new quarters. Also, the adults may be killed off, but viable eggs may remain after fumigation.

A species which has similar habits to this species and is frequently found in the same places in other areas is *Trogium pulsatorium* (Linnaeus). It has become widespread and it is expected that it will become established in Hawaii. It has not yet been found here to my knowledge, however. It has minute fore wings and the body is marked with dark dots and patches.

Family PACHYTROCTIDAE Pearman, 1936:60

Genus **PSYLLONEURA** Enderlein, 1903

Karny assigns the genus to the Rhypsocini of the Empheriini, which he places in the "Trogidae."

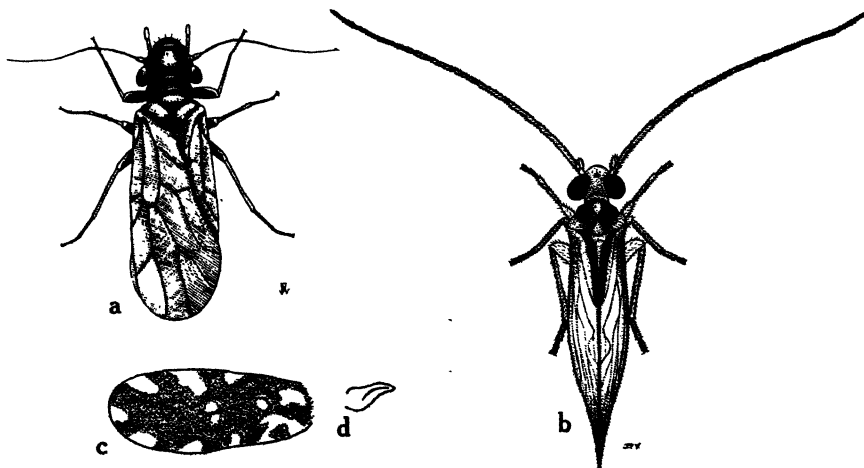


Figure 126—**a**, *Psylloneura williamsi* Banks; **b**, *Caecilius analis* Banks; **c-d**, fore and hind wings of *Psoquilla margine-punctata* Hagen. (**a** and **b** from original drawings by Williams and Yamamoto for Banks, 1931.)

Psylloneura williamsi Banks (figs. 122, e; 126; 127, a).

Psylloneura williamsi Banks, 1931:439, pl. 7, figs. 8, 9; pl. 8, fig. 6; pl. 9, fig. 7 (eggs).

Oahu (type series from Ewa and Waialua).

Immigrant, but source unknown.

The type series was collected from sugarcane.

Banks' figure of the venation of the hind wing is erroneous and misleading. Vein R_{2+3} is not vertical, but it is oblique; the anal vein is not as dark and heavily developed as the others; the axillary vein is present. These omissions as well as others including the proper shapes of the wings are herein corrected by new figures which were made from specimens from the type series.

This species folds its wings flat over its body when at rest. Williams (1931:88) says, "It lays its eggs singly; these are about 0.45 mm. long and rather slender oval and more or less covered with tiny bits of excrement. It has been found tolerably common on sugarcane trash"

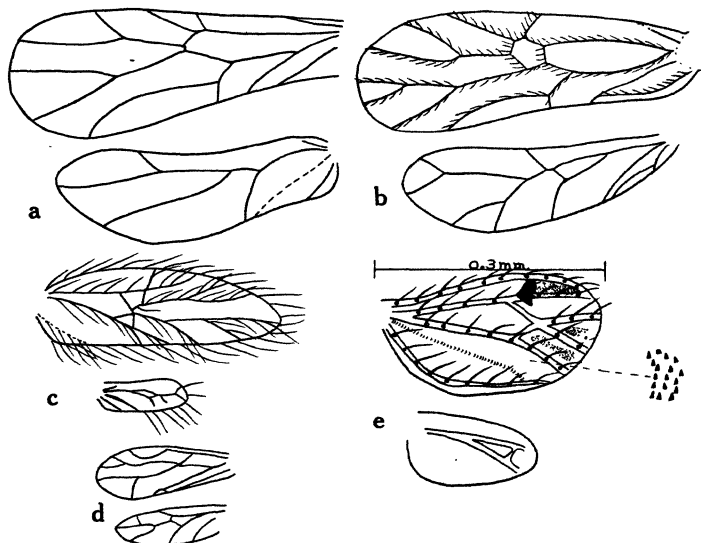


Figure 127—Sketches of some psocid wings: a, *Psylloneura williamsi* Banks; b, *Psyllipsocus minutissimus* (Enderlein); c, *Psocathropos lachlani* Ribaga; d, *Hageniella solitaria* Banks (copied from Banks, 1931, and not checked with specimens); e, *Chactopsocus richardsi* Pearman.

Family PSOCATHROPIDAE Pearman, 1936:60

KEY TO THE GENERA FOUND IN HAWAII

1. Hind wings nearly as long as fore wings, without marginal setae; fore wings as illustrated, setae on veins moderate in length, but without marginal setae. **Psyllipsocus** Selys.

2. Hind wings much reduced, with some long marginal setae; fore wings as illustrated, bristling with very long setae, and margins with very long bristles.....**Psocathropos** Ribaga.

Genus **PSYLLIPSOCUS** Selys, 1872

Psyllipsocus minutissimus (Enderlein) (fig. 127, b).

Parempheria minutissima Enderlein, 1920:458. Takahashi, 1938:11, redescription. Gurney, 1943:203-205, nomenclature.

Oahu (type locality: Koolau Mountains).

Immigrant. Takahashi (1938:12) recorded this species as rather common in dwellings in Formosa.

To my knowledge, this species has not been recorded in Hawaii since it was described from a unique female. I found it among molds growing on a bottle of rum in a cupboard at Punaluu, Oahu, in 1943. It is a distinct, delicate little species which should not be confused with any of our other psocids.

Genus **PSOCATHROPOS** Ribaga, 1899

Psocathropos lachlani Ribaga (fig. 127, c).

Psocathropos lachlani Ribaga, 1899:158, pl. 7.

Oahu.

Immigrant. Described from an Italian hothouse and now also known from Africa. First found by Swezey in Honolulu in 1927.

This peculiar little species is an active and agile jumper and can leap several inches—a prodigious distance for such a minute creature. When jumping on paper, it can be heard more easily than seen. It is recognized easily by its clear wings, which have unusually long bristle-like hairs on the veins and wing margins, and by its pale body. It has at times been abundant about books in my laboratory and home and appears to reproduce rapidly in damp weather. I believe that this is the species I once found in numbers on a pair of moldy boots in Honolulu. Excellent control has been obtained by cyanide fumigation, and naphthalene is a good repellent and will kill the psocids in closed compartments.

Family **CAECILIIDAE** Kolbe, 1884

Two genera are included here. Each of these has two-segmented tarsi, fore wings with setose veins and margins and the areola postica present. I have not seen *Hageniola*, and I am not sure that it should be included here, although it was assigned to the Caeciliinae by Banks when it was described. Karny (1930) places *Caecilius* in the Lachesillini of the Lachesillidae.

KEY TO THE GENERA OF CAECILIIDAE FOUND IN HAWAII

1. Media of fore wings with two branches (fig. 130, b)..... **Caecilius** Curtis.
2. Media of fore wings with only one branch (fig. 127, d)..... **Hageniola** Banks.

Genus **CAECILIUS** Curtis, 1837

This genus is almost cosmopolitan in distribution. In addition to the species recorded below, I have seen specimens of another as yet unidentified species.

Caecilius analis Banks (figs. 122, a; 126, b; 130, b, c).

Caecilius analis Banks, 1931:437, pl. 7, fig. 2; pl. 8, fig. 2; pl. 9, fig. 3 (eggs).

Oahu (type locality). (It is probably present on other islands, but it has been neglected by collectors.)

Immigrant. This species is also known from the Marquesas, and it will probably be found to be widespread.

It has been found on sugarcane, *Cheirodendron* and other trees and shrubs; I found it abundant on various shrubs on the summit of Mount Konahuanui in May, 1943 (altitude over 3,000 feet). In life it is mostly pale lemon-yellowish with black eyes, with the antennae pale at the base but becoming fuscous distad. the area between the axillary vein and hind margin of the fore wings fuscous, and some variable fuscous marks on the thoracic nota, the latter markings rather extensive on some examples.

Genus **HAGENIOLA** Banks, 1931:438

This genus is known thus far only from the Hawaiian Islands, but its discovery elsewhere depends only upon further collecting or the study of undetermined collections. I have seen no representatives of the genotype, and from the figures given by Banks, it appears very different from any other genus known from our fauna. It may not be correctly placed here.

Hageniola solitaria Banks (fig. 127, d).

Hageniola solitaria Banks, 1931:438, pl. 7, fig. 5. Genotype.

Oahu (type locality: Honolulu).

Immigrant. Source unknown.

The type was collected on sugarcane.

Family PERIPSOCIDAE Karny, 1930

KEY TO THE GENERA FOUND IN HAWAII

1. Wings reduced as in figure 127, e. **Chaetopsocus** Pearman.
2. Wings fully developed for flight. **Ectopsocus** McLachlan.

Genus **CHAETOPSOCUS** Pearman, 1929:105

When Pearman described this genus he considered it allied to *Trichopsocus* Kolbe, 1882. However, later he obtained additional material, found that he had mistaken its characters and relationships and submerged it with *Ectopsocus*. He said (1942:291) that it was allied to "*Ectopsocus*, from the genotype of which, however, it differs in some significant respects." In spite of its different characters and appearance, Pearman thought that it would be best to sink *Chaetopsocus* until more comparative morphological studies could be completed and "until it is known whether it will typify a particular segregate. . . ." Pearman's *richardsi* differs so greatly in structure, facies and habit from our species of *Ectopsocus* that I believe that it would be misleading and illogical to place the two groups together in this manual, although it may be a flightless *Ectopsocus* derivative.

Chaetopsocus richardsi Pearman (fig. 127. e).

Chaetopsocus richardsi Pearman, 1929:105, figs. 1, a-d.

Ectopsocus richardsi (Pearman) Pearman, 1942:290 (corrected redescription).

Oahu.

Immigrant. Not reported from Hawaii before, but first found in Hawaii in 1943 by J. S. Rosa at Honolulu in large numbers in a package of beans imported from North America. It was originally described from one adult female and one nymph taken from West African cacao on a London wharf, and later (Pearman, 1942:290) it was found in cacao at Winnebah, Gold Coast.

This is a minute and peculiar psocid about 1.5 mm. long. There is no other psocid in Hawaii which might be confused with this strange species. It has a dark brown head, the fore wings are only 0.3 to 0.4 mm. long, the venation is difficult to trace, and there is a tendency toward variation in both pairs of wings. All the specimens I have seen are micropterous, but Pearman found that "some females have wings of greater length, in a few cases of nearly full development with complete Ectopsocid venation." The type has short wings, the fore pair of which does not reach the posterior margin of the third abdominal segment. Some males and females examined by Pearman had longer wings that extend farther caudad, but not beyond the middle of the abdomen, and 10 percent of the females had the wings "Extending beyond middle of abdomen but not, or barely, beyond its apex."

Genus **ECTOPSOCUS** McLachlan, 1899

Some workers place this genus in the Caeciliidae. The fore wings lack the areola postica and have at most minute and inconspicuous hairs on the veins and the marginal setae are microscopic or apparently absent. The tarsi are two-segmented.

In addition to the three following species, I have seen and collected other apparently undescribed species of this genus in the Hawaiian Islands. Two of the three species recorded from Hawaii heretofore have not been reported elsewhere, but I have collected all three of them outside the Hawaiian Islands. They have evidently been spread widely over the Pacific through the aid of commerce. The genus is almost cosmopolitan.

KEY TO THE SPECIES OF ECTOPSOCUS FOUND IN HAWAII

1. Fore wing clear or slightly embrowned, without any color pattern (fig. 129, b)..... **hawaiiensis** Enderlein.
Fore wing dark, with conspicuous pale markings..... 2
2. Fore wing with a transverse pale band near base entirely across the wing as in figure 129, c-d..... **fullawayi** Enderlein.
Fore wing without such a pale subbasal band, with at most a pale basal patch in the anal and axillary cells as in figure 129, a..... **perkinsi** Banks.

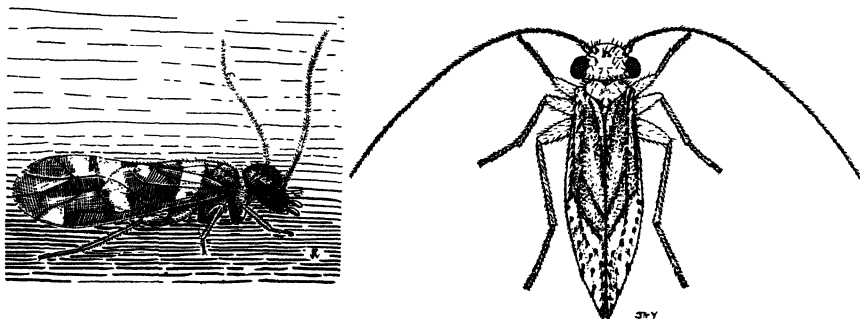


Figure 128—*Ectopsocus fullawayi* Enderlein, left; *Hemipsocus roseus* (Hagen), right. (From original drawings by Williams and Yamamoto for Banks, 1931.)

Ectopsocus fullawayi Enderlein (figs. 122, d; 128; 129, c-d).

Ectopsocus fullawayi Enderlein, 1913:356.

Oahu (type locality: Honolulu), Laysan.

Immigrant. I collected this species at light at the Naval Station at Tutuila, Samoa, in 1940; and in 1934 at Tubuai, Austral Islands, at Pitcairn Island, Oeno Island, Henderson Island and Mangareva Island. All of these extra-Hawaiian locality records are new, and, with the exception of Samoa, are in southeastern Polynesia.

Hostplants: *Acacia confusa*, *Acacia koa*, sugarcane, sweet potato.

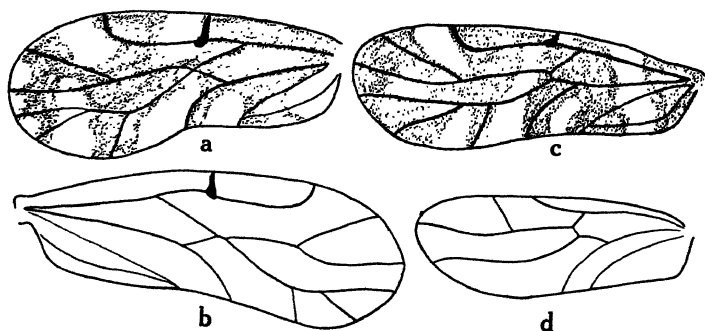


Figure 129—Wings of *Ectopsocus*: a, fore wing of *E. perkinsi* Banks; b, fore wing of *E. hawaiiensis* Enderlein; c-d, fore and hind wings of *E. fullawayi* Enderlein.

***Ectopsocus hawaiiensis* Enderlein (fig. 129, b).**

Ectopsocus hawaiiensis Enderlein, 1913:356.

Oahu (type locality: Honolulu).

Immigrant. I collected specimens of this species at light at the Naval Station, Tutuila, Samoa, in 1940 (new record) and I have seen four examples taken by F. X. Williams in the quarantine room of the Hawaiian Sugar Planters' Experiment Station in Honolulu and labeled "Philippines ???." Swezey and Usinger collected it on Guam.

This is one of our commonest species and has been found on *Ficus*, pineapple, smutty "noni" and moldy *Pandanus* mats, and I have recently examined a series of specimens reared from old pods of pigeon peas by Swezey and have seen it commonly under webblings on *Ficus bengalensis* where it becomes especially abundant when the young of the aphid *Thoracaphis* are produced in winter.

***Ectopsocus perkinsi* Banks (fig. 129, a).**

Ectopsocus perkinsi Banks, 1931:438, pl. 7, fig. 4.

Oahu (type locality: "Honolulu Mts. 1500 ft.").

Immigrant. I collected what appears to be this species on Viti Levu, Fiji, in 1938 (new record).

F. X. Williams found some examples in new garden compost.

Family HEMIPSOCIDAE Pearman, 1935

One genus from our fauna is placed here. If it were not for its setose fore wing veins and the fact that media in the fore wing has only one branch so that there are only two marginal cells beyond the cubital cell, it might run to the Psocidae. Banks places the genus in the Caeciliidae, and Karny places it in Hemipsocini and assigns it to the Psocidae.

Genus **HEMIPSOCUS** Selys, 1872

Hemipsocus roseus (Hagen) (figs. 122, b-c; 128; 130, a).

Psocus roseus Hagen, 1859:203.

Epipsocus roseus (Hagen) McLachlan, 1872:78.

Hemipsocus roseus (Hagen) Banks, 1931:438, pl. 8, fig. 1; pl. 9, figs. 1, 2 (eggs).

Oahu.

Immigrant. Ceylon, Philippines, Central America, West Indies. First recorded from Honolulu by Banks in 1931 from specimens collected a few years previously.

This is one of the most distinct of our immigrant species. The large, conspicuous setae on the fore wing veins arise from conspicuous dark dots which give the wings a characteristic spotted appearance. In life the integument is almost white, but the sides of the body, including the head, thorax and abdomen, are speckled with pink blotches, and the eyes are greenish.

This insect has been taken from sugarcane and other plants; it is common beneath the dried leaf-sheaths of sugarcane. Williams (1931:86) says, "The female lays a group of tiny eggs and they are protected by a convex cover that greatly resembles a speck of mud. One specimen was reared from an egg, the life cycle occupying about 31 days. The adults may live for many weeks."

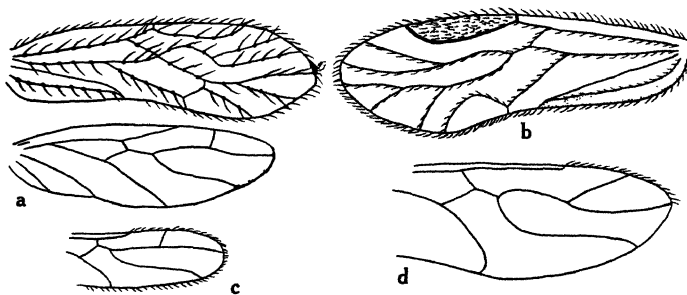


Figure 130—Venation of some psyllid wings: a, fore and hind wings of *Hemipsocus roseus* (Hagen); b, fore wing of *Caecilius analis* Banks; c, distal part of hind wing of *Caecilius analis* Banks for comparison with d; d, the same of *Palistreptus montanus* (Perkins) to show differences in marginal setae.

Family **ELIPSOCIDAE** Pearman, 1936:60

Two endemic genera are placed here. Some authors include them with the Caeciliidae, and Karny placed them in the Elipsocinae of the Lachesillidae. Both *Kilaella* and *Palistreptus* have the apex of cubitus in the hind wing characteristically curved into the wing margin as illustrated (figs. 131, 132). These genera have three-segmented tarsi and the fore wing veins and margins are setose.

KEY TO THE GENERA OF ELIPSOCIDAE FOUND IN HAWAII

1. Fore wing with radial sector and media not fused into a distinct common vein, but joined by a short transverse cross-vein (fig. 131, g) or just touching one another and forming a simple X (fig. 131, h).....**Kilaueella** Enderlein.
2. Fore wing with radial sector and media completely fused to form a single, short, distinct, longitudinal vein between their points of contact and their points of divergence which is several times as long as breadth of a vein (fig. 132).....**Palistreptus** Enderlein.

Because of the fusion of radial sector and media in the fore wing, *Palistreptus* might be confused with *Caecilus* by one unfamiliar with the group, but the three-segmented tarsi, the fact that in the hind wing R_{2+3} is more than one-half as long as R_{4+5} instead of only about one-fourth as long, the non-setose hind margin of the hind wing, together with other characters, will all serve to distinguish the two genera easily.

Genus **KILAUELLA** Enderlein, 1913:357

In *Fauna Hawaiensis* Perkins described 10 endemic species in the genus *Elipsocus*. All these species have since been removed from that genus by Enderlein and are now placed in either *Kilaueella* or *Palistreptus*. These two genera are known only from the Hawaiian Islands, but their affinities appear to be with other Polynesian psocids.

Enderlein (1920) considered that *Kilaueella* consisted of a single species with five varieties, and he reduced two of Perkins' species to synonymy.

At least one of the species of *Kilaueella* shares with *Palistreptus* (see below) an unusual and confusing tendency toward variation in wing venation. The normal condition in the fore wing of *Kilaueella* is that areola postica is completely free from media. However, on the specimens of *K. micramaura* which I have seen, areola postica is joined to media in the same way that it is in the Hawaiian *Psocus*. Enderlein (1920, fig. 10) illustrates a specimen which he called *K. micramaura* which does not have areola postica fused with media. Perkins, in his original description, stated that areola postica was fused with media and that "This minute species is easily distinguished by the form of the area postica, and the nervuration is not that of the genus *Elipsocus* at all. Nevertheless I have not cared to separate it, because of the fact that other species have a tendency towards a similar nervuration, e.g. *E. inconstans* . . ." (For *E. inconstans*, see *Palistreptus inconstans*, below.) Banks (1931:437), noting the discrepancy between Perkins' original description and Enderlein's figure, said, "I give a figure of my specimen which agrees closely with Perkins'; the figure of Enderlein is of another species; Perkins distinctly mentions the union of areola postica with media." Banks' figure agrees in venation with the specimens I have seen, including material in Perkins' own collection and that of the *Fauna Hawaiensis*. However, it appears to me that Enderlein's figures have been mislabeled (see discussion below under *inaequifusca* for my reasons).

If the venation of *Kilauella micramaura* were proven to be constant for the fusion of areola postica and media (and it has not yet been demonstrated to be otherwise, for all of the specimens studied have it constant), then I believe that a new genus would be necessary for the species. I believe we can see here a genus or genera "in the making." As it is, *Kilauella micramaura* probably cannot be assigned to the genus *Kilauella* on the basis of wing venation unless the usually diagnostically important character of the areola postica is ignored.

The following table of identification is a tentative key to the species (in the sense of Perkins). I have not seen any specimens of *K. criniger*, which was described by Perkins from a unique, and have been unable to place it in the key. According to Perkins, it is much like *K. psylloides*, but has some definite fuscous markings.

In addition to the following species, I have studied other forms which appear to be distinct new species.

KEY TO THE SPECIES OF KILAUELLA

(*K. criniger* [Perkins] omitted)

1. Hind wing with vein R_{2+3} almost vertical (as in fig. 131, e); fore wing with vein R_{2+3} diverging at a point close above origin of vein M_2 and areola postica completely fused with media (fig. 131, d)..... **micramaura** (Perkins).
Hind wing with vein R_{2+3} very oblique (fig. 131, a); fore wing with veins R_{2+3} and R_{4+5} diverging at a point closer to origin of vein M_2 than to M_3 and areola postica not fused with media (fig. 131, a)..... 2
- 2(1). Fore wing with areola postica just touching or very nearly touching media—but not fused with it—as in figure 131, f..... **frigida** (Perkins).
Fore wing with areola postica completely free from media (separated by a distance at least twice as great as thickness of media) (fig. 131, a)..... 3
- 3(2). Pterostigma of fore wings with a distinct pink spot of variable size at base and apex, or entire pterostigma pink..... **erythrodicta** (Perkins).
Pterostigma without pink coloration (excepting an occasional faint tinge of pink at base only, but never at apex)..... 4
- 4(3). Fore wings with veins R and M touching one another below base of pterostigma and there forming a simple X (fig. 131, h)..... **debilis** (Perkins).
Fore wings with veins R and M not touching but connected by a short cross-vein as in figure 131, g..... 5
- 5(4). Membrane of fore wings almost entirely hyaline, at most only a few parts infusate; areola postica variable, but shaped more like that shown in figure 131, b, than that in figure 131, c..... **psylloides** (Perkins).
Membrane of fore wings almost entirely infusate, at most only parts hyaline; areola postica variable, but shaped more like that shown in figure 131, c, than in figure 131, b... 6

- 6(5). Fore wings with areola postica uniformly infusate throughout *vinosa* (McLachlan).

Fore wings with at least the basal part of areola postica pale or subhyaline *inaequifusca* (Perkins).

Because I have found among the various species described by Perkins characters adequate enough to enable me to prepare this key, I have not accepted Enderlein's arrangement of the species of this genus. A synopsis of Enderlein's classification is given following the main list of species.

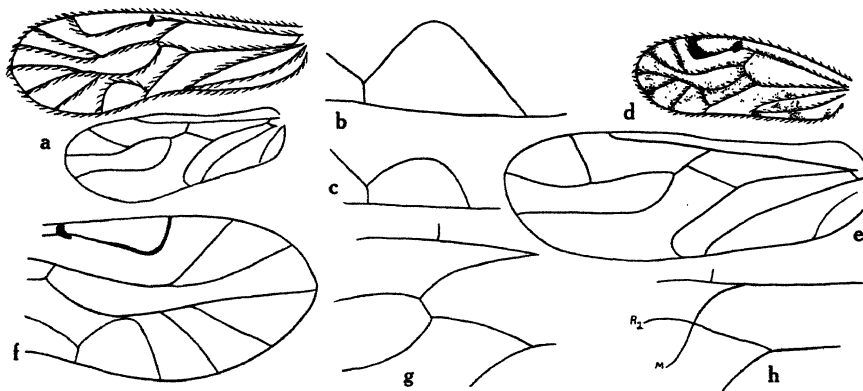


Figure 131—Details of *Kilaueella* species: a, fore and hind wings of *K. vinosa* (McLachlan); b, areola postica of *K. psylloides* (Perkins); c, areola postica of *K. inaequifusca* (Perkins); d, fore wing of *K. micramaura* (Perkins); e, hind wing of *K. micramaura* (not to same scale as d); f, apical part of fore wing of *K. frigida* (Perkins) to show formation of areola postica, setae omitted; g, formation of junction of R and M in fore wing of *K. psylloides* (Perkins); h, the same for *K. debilis* (Perkins).

***Kilaueella criniger* (Perkins).**

Elipsocus criniger Perkins, 1899:85.

Kilaueella criniger (Perkins) Enderlein, 1913:357.

Endemic. Hawaii (type locality: Kona, 2,000 feet).

I have not seen authentic specimens of this species. Perkins said that it was an ally of *K. psylloides*. Enderlein (1920:456) reduced it to a synonym of *K. psylloides*. Specimens thought to be this species were taken by Swezey on *Suttonia* and *Sophora*.

***Kilaueella debilis* (Perkins) (fig. 131, h).**

Elipsocus debilis Perkins, 1899:85.

Kilaueella debilis (Perkins) Enderlein, 1913:357.

Kilaueella vinosus variety *debilis* (Perkins) Enderlein, 1920:455, fig. 12.

Endemic. Oahu (type locality: Waianae Mountains, above 2,000 feet).

This form appears to me to be extremely close to *K. psylloides*, and it may be the same. The type must be restudied before a decision can be reached, however. Banks (1931:437) said, "Fully distinct from *K. vinosa*."

***Kilauella erythrosticta* (Perkins).**

Elipsocus erythrosticta Perkins, 1899:86.

Kilauella erythrosticta (Perkins) Enderlein, 1913:357. Genotype of *Kilauella*.

Kilauella vinosa variety *erythrosticta* (Perkins) Enderlein, 1920:454, fig. 9.

Endemic. Oahu, Hawaii (type locality: Kona, 2,000 feet).

I have seen specimens of this beautiful species taken from *Elacocarpus*, *Pisonia*, *Antidesma*, *Pelca*, and *Neowawraca*. The pink color of the pterostigma is striking and diagnostic.

***Kilauella frigida* (Perkins) (fig. 131, f).**

Elipsocus frigidus Perkins, 1899:87.

Kilauella frigida (Perkins) Enderlein, 1913:357.

Synonymized with *K. micramaura* by Enderlein, 1920:455.

Endemic. Hawaii (type locality: Mount Hualalai, 8,000 feet).

***Kilauella inaequifusca* (Perkins) (fig. 131, c).**

Elipsocus inaequifuscus Perkins, 1899:86.

Kilauella inaequifusca (Perkins) Enderlein, 1913:357.

Kilauella vinosa variety *inaequifusca* (Perkins) Enderlein, 1920:456, fig. 11 (10 ?).

Endemic. Maui (type locality: Mount Haleakala, 5,000 feet).

Enderlein's figure is not of this species, but it seems to represent *K. micramaura*. It appears likely to me that the names attributed to figures 10 and 11 of Enderlein's plate 6 have been confused and should be transposed.

***Kilauella micramaura* (Perkins) (fig. 131, d-e).**

Elipsocus micramaurus Perkins, 1899:87.

Kilauella micramaura (Perkins) Enderlein, 1913:357.

Kilauella vinosa variety *micramaura* (Perkins) Enderlein, 1920:455, fig. 10.

Endemic. Oahu, Hawaii (type locality: Kona, 4,000 feet).

This species has been collected from *Metrosideros* and *Gouldia*, and I have seen an example taken by Swezey from fruit of the Sabal palmetto in Honolulu—the only record I have for the occurrence of the species outside of the forest.

Banks (1931:437, pl. 7, fig. 7) considered this to be a distinct species, and he figured his specimen. He considers Enderlein's figure as that of another species, and he appears to be correct in that assumption. I have seen several specimens of this species, and none of them agrees with Enderlein's figure. However, as mentioned above, there may be some confusion in the labeling of Enderlein's figures 10 and 11 (see discussion under *K. inaequifusca*).

Kilauella psylloides (Perkins) (fig. 131, b, g).

Elipsocus psylloides Perkins, 1899:85.

Kilauella psylloides (Perkins) Enderlein, 1913:357.

Kilauella vinosa variety *psylloides* (Perkins) Enderlein, 1920:456.

Endemic. Oahu, Maui, Hawaii (type locality not specifically designated by Perkins), Midway (?).

This species has been found on *Cheirodendron*, *Xylosma*, *Pelea* and *Santalum*. It appears to me that this may be only a form of *debilis*.

Kilauella vinosa (McLachlan) (fig. 131, a).

Elipsocus vinosus McLachlan, 1883:229. Perkins, 1899:86.

Kilauella vinosa (McLachlan) Enderlein, 1913, 357; 1920:453, fig. 8.

Endemic. Maui, Hawaii (type locality not specifically designated by Perkins). Recorded from *Suttonia* and *Styphelia* (*Cyathodes*).

I have seen specimens from Maui and Hawaii only, but Perkins (1899:86) said that it occurred on "many and probably all of the islands, in the forests."

According to Enderlein's opinion (1920), the arrangement of the genus *Kilauella* would be as follows:

Kilauella vinosa (Perkins) Enderlein.

Kilauella vinosa variety *erythrosticta* (Perkins) Enderlein.

Kilauella vinosa variety *micramaura* (Perkins) Enderlein.

Kilauella frigidus (Perkins); synonymy by Enderlein, 1920:455.

Kilauella vinosa variety *debilis* (Perkins) Enderlein.

Kilauella vinosa variety *inaequifusca* (Perkins) Enderlein.

Kilauella vinosa variety *psylloides* (Perkins) Enderlein.

Kilauella criniger (Perkins); synonymy by Enderlein, 1920:456.

Enderlein may be more correct in his classification of the group than Perkins, but I believe that a much more detailed study based upon longer series of specimens and including critical examination of the holotypes and the genitalia of every form

is essential before anyone will be in a position to show the true condition existing in this group. Some of these forms appear to be fully distinct species, and, moreover, their appearance in the field certainly leads one to believe that several to many species are involved here.

Genus **PALISTREPTUS** Enderlein, 1920:457

This genus is a close ally of *Kilaueella* and appears to me to be but a slightly differentiated offshoot group of *Kilaueella*. It might be better to consider this group as only a subgenus of *Kilaueella*. The fusion of the radial sector and media in the fore wings is somewhat variable. Some specimens have the single vein formed by this fusion shorter on one wing than on the other. I have seen some specimens of *Kilaueella* that have a tendency toward this type of venation, but none that has it so completely developed. Most specimens of both of the species included here are larger than most of the species of *Kilaueella* and to the naked eye they more nearly resemble species of *Psocus*. The fused section of the radial sector and media in the fore wings resembles the structure of *Caccilius*, and this group might be confused with *Caccilius*. However, the three-segmented tarsi alone will readily distinguish *Palistreptus*. In this genus, too, the hind wings do not have the hind margins setose as in *Caccilius* (see fig. 130). They are true forest insects.

KEY TO THE SPECIES OF PALISTREPTUS

1. Fore wing with areola postica partially or entirely infusate; infuscations of wing membrane numerous, distinct, usually quite dark and giving wing a conspicuously speckled and maculate appearance; postclypeus coarsely reticulate and dull **inconstans** (Perkins).
2. Fore wings with areola postica hyaline, never distinctly infusate; infuscations of wing membrane faint and comparatively few, wing faintly spotted, but not conspicuously and contrastingly speckled or maculate; postclypeus finely alutaceous and moderately shiny..... **montanus** (Perkins).

Palistreptus inconstans (Perkins) (figs. 132; 133, a-f).

Elipsocus inconstans Perkins, 1899:84.

Kilaueella inconstans (Perkins) Enderlein, 1913:307.

Palistreptus inconstans (Perkins) Enderlein, 1920:457, figs. 14-15. Genotype.

Endemic. Kauai, Oahu, Molokai, Maui, Lanai, Hawaii (type locality not designated in original descriptions).

This species has been found on *Metrosideros* and other forest trees and on Jerusalem cherry.

Perkins chose a good name for this species—it is unusually variable. In his original description, Perkins (1899) said,

The area postica is sometimes free, with a distinct space between it and the inner branch of the cubitus, but sometimes its vertex touches (or is connected by an excessively short transverse nervule with) that branch. In the latter case a closed discoidal area is formed and the examples have no longer the nervuration of the genus. This variation is exhibited by examples of the most different superficial appearance, as well as in those of similar general aspect, and the nervuration on the two sides of the same insect may be markedly different, so that it is evidently in a very unstable condition. Examples from the most widely separated islands of the group show analogous variation.

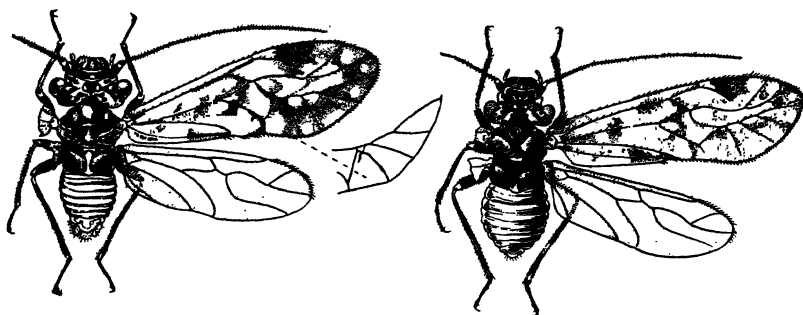


Figure 132—A pair of *Palistreptus inconstans* (Perkins) from Kona, Hawaii, 4,000 feet, from the type series. (Abernathy drawings.) I have sketched an insert figure between the two to show a variation of venation in another example.

I have made some camera lucida sketches from several specimens collected by Perkins to illustrate the confusing variability of the areola postica. Most of the specimens examined have the areola postica free, and this appears to be the "normal" condition. On some examples the sides of the front of the head are conspicuously angulate or actually produced as a distinct tubercle between the eyes and the antennae. I have not seen such protuberances on any of the specimens of *Palistreptus montanus* examined.

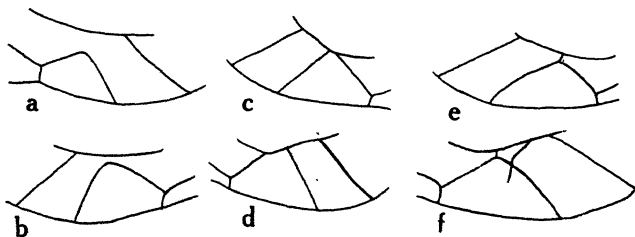


Figure 133—Sketches to show variation in form of areola postica of *Palistreptus inconstans* (Perkins); a, the "normal" form; b, another example; c-d, right and left wings of one individual; e-f, right and left wings of another individual.

Palistreptus montanus (Perkins) (fig. 130, d).

Elipsocus montanus Perkins, 1899:83.

Kilauella montana (Perkins) Enderlein, 1913:359.

Palistreptus inconstans variety *montanus* (Perkins) Enderlein, 1920:458, fig. 16.

Endemic. Maui (type locality: Mount Haleakala, 5,000 feet).

All the specimens that I have seen may be distinguished readily from typical *inconstans*. None of the dozen examples studied has any tendency toward variation of areola postica as has *inconstans*. I have been unable to find any differences in the male genitalia between this form and *inconstans* in the dissections I have made of one specimen of each form, but perhaps my preparations have not been adequate.

Family PSOCIDAE Leach, 1815

This family contains the largest of the Hawaiian psocids. The two-segmented tarsi, well-developed pterostigma, naked fore wing veins, the fact that areola postica is joined to media and other characters will serve to distinguish the forms present in Hawaii. However, there are certain aberrant and confusing species of Elipsocidae, namely *Kilauella micramaura* and *Palistreptus inconstans*, which vary in their wing venation and may be confused with this family. Each of these species has individuals in whose fore wings the areola postica may be fused with media just as in *Psocus*. However, these species have the wing veins distinctly setose and their tarsi are three-segmented instead of two-segmented as they are in *Psocus*.

Perkins, in *Fauna Hawaiënsis*, described 14 species, none of which was figured. to that genus and it is not figured. I have not seen it, and I cannot place it as to genus or species in this system. It is, however, placed tentatively at the end of *Psocus*.

Genus PSOCUS Fabricius, 1798

This cosmopolitan genus contains the largest species of Hawaiian psocids—some of them measure a centimeter in expanse. Also, in numbers of species described, this genus is the largest. All of the species recorded are endemic to these islands and are denizens of the forests where they can commonly be collected from shrubbery, dead branches, mossy limbs, trunks of trees and similar situations. In some localities they are among the commonest of native insects and occur in swarms.

Perkins, in *Fauna Hawaiënsis*, described 14 species, none of which was figured. In 1920, Enderlein reduced Perkins' species to two full species including six varieties—the other six species of Perkins were considered synonyms. Enderlein gave colored illustrations of seven of these forms. Supposedly, Enderlein studied Perkins' types, but there is reason to believe that he made certain errors and did not have the actual holotype specimen before him in every case. Banks, who has available some of Perkins' original material (from the *Fauna Hawaiënsis* collection) at the Museum of Comparative Zoology at Harvard, does not agree with Enderlein's synonymy. In a box of miscellaneous psocids sent to the Bishop

Museum by Dr. Perkins, there appears the following note written by Perkins: "NB. The named specimens of psocids here are not altogether to be relied on. The *types* in B[ritish] Mus[eum] were all named and labeled as such by myself, but the collection in general was blocked up later by a boy who in some cases at least to my knowledge made errors when he did this and put on the printed labels, after I had returned to Hawaii." One can understand, therefore, that errors might easily be made when examining *Fauna Hawaiiensis* psocid material other than the actual types labeled by Perkins. However, Enderlein definitely states that each of his figures of *Psocus* was made "Nach der Type."

It may be that Enderlein's interpretation is more nearly correct than that of Perkins. However, I believe that a more detailed study of this group with a careful re-examination of the holotypes and a study of adequate series is essential before we can hope to understand this endemic complex. Perkins had the great advantage of knowledge gained by studying the insects in the field, and I must say that various forms which I have collected and others which I have studied certainly appear to be distinct species. It is probable that a study of the genitalia will reveal some useful data. I have tried to make a key to the species from the Bishop Museum's share of the *Fauna Hawaiiensis* material, but I have failed to find usable external characters in my cursory study. I have, however, been handicapped by not having a complete set of the species available. Evidently most of the "species" have unusually variable color patterns in the wings. In some series, hardly any two specimens agree as to color pattern. The drawings of the wings of the types, which were made after this text was completed, will aid in the identification of the various forms.

The 14 species are listed first as they were described by Perkins, and, following this list, the arrangement proposed by Enderlein is given in synoptic form.

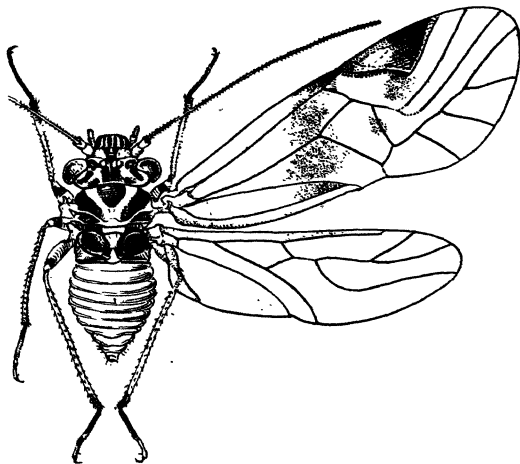


Figure 134—*Psocus haleakalae* Perkins. (Abernathy drawing.)

Psocus distinguendus* Perkins (fig. 135, a).Psocus distinguendus* Perkins, 1899:80.*Clematostigma distinguendum* (Perkins) Enderlein, 1913:355.

Endemic. Molokai (type locality: "Molokai Mts., 3,000 ft., June, 1896"), Lanai, Maui, Hawaii.

Hostplants: *Acacia koa*, *Coprosma*, *Metrosideros* and *Sadleria*.

Psocus haleakalae* Perkins (figs. 134; 135, b).Psocus haleakalae* Perkins, 1899:77.*Clematostigma haleakalae* (Perkins) Enderlein, 1913:355.

Endemic. Maui (type locality: Mount Haleakala, 5,000 feet, May, 1896), Hawaii.

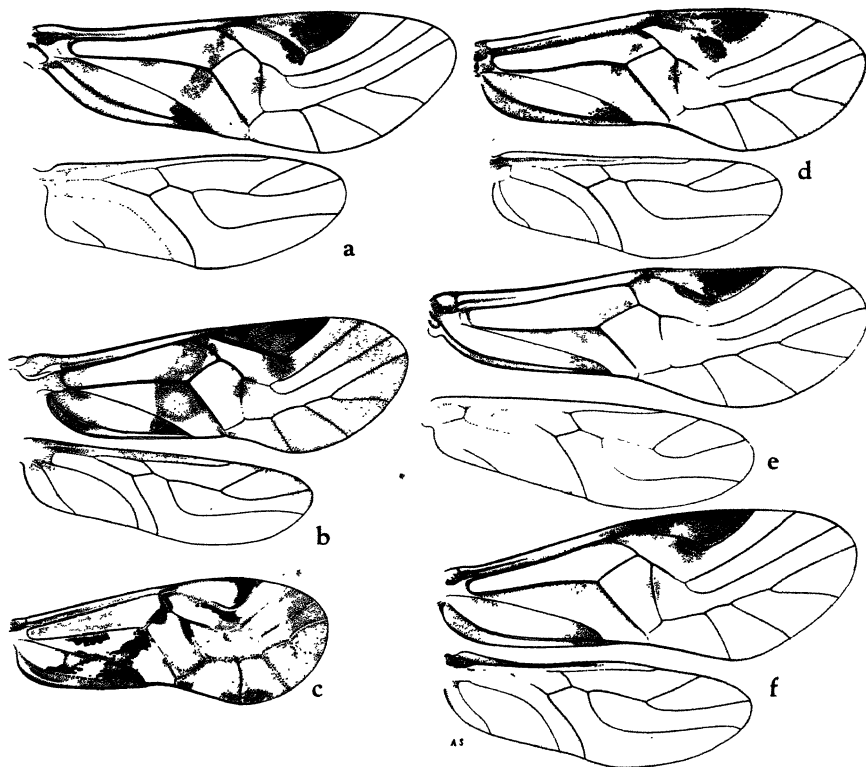


Figure 135—Wings of holotypes of *Psocus*: a, *P. distinguendus* Perkins, male; b, *P. haleakalae* Perkins, male; c, *P. heterogamias* Perkins, male; d, *P. hualalai* Perkins, male; e, *P. kauaiensis* Perkins, male; f, *P. konae* Perkins, male. (Drawn at the British Museum of Natural History by Smith.)

Psocus heterogamias Perkins (fig. 135, c).*Psocus heterogamias* Perkins, 1899:82.*Clematostigma heterogamias* (Perkins) Enderlein, 1913:355.

Endemic. Oahu (type locality: Waianae Mountains, April, 1892).

Hostplant: *Elaeocarpus*.**Psocus hualalai** Perkins (fig. 135, d).*Psocus hualalai* Perkins, 1899:79.*Clematostigma hualalai* (Perkins) Enderlein, 1913:355.

Endemic. Hawaii (type locality: Mount Hualalai, "about 8000 feet," August, 1892).

Psocus kauaiensis Perkins (fig. 135, e).*Psocus kauaiensis* Perkins, 1899:79.*Clematostigma kauaiensis* (Perkins) Enderlein, 1913:355.

Endemic. Kauai (type from 4,000 feet?), Oahu, Maui.

Hostplant: *Metrosideros*.

Banks has recorded this species erroneously from the island of Guam (1942:25). I have examined the series of Guam specimens determined by him as this species and find them to be quite distinct although the characters displayed by the wings are remarkably similar. The genitalia afford excellent characters for separating the species. It may also be that the Guam series represents two species instead of one as determined by Banks.

Psocus kona Perkins (fig. 135, f).*Psocus kona* Perkins, 1899:79.*Clematostigma kona* (Perkins) Enderlein, 1913:355.

Endemic. Hawaii (type locality: Kona, 4,000 feet, 1892).

Psocus lanaiensis Perkins (fig. 136, a).*Psocus lanaiensis* Perkins, 1899:81.*Clematostigma lanaiensis* (Perkins) Enderlein, 1913:355.

Endemic. Molokai, Lanai (type locality: Koele Mountains, 3,000 feet, February, 1894).

Psocus molokaiensis Perkins (fig. 136, b).*Psocus molokaiensis* Perkins, 1899:80.*Clematostigma molokaiensis* (Perkins) Enderlein, 1913:355.

Endemic. Molokai (type locality: 3,000 feet, June, 1896).

Hostplant: *Styphelia* (*Cyathodes*).**Psocus monticola** Perkins (fig. 136, c).*Psocus monticola* Perkins, 1899:82.*Clematostigma monticola* (Perkins) Enderlein, 1913:355.

Endemic. Kauai (type locality. Waimea Mountains, 4,000 feet, 1894).

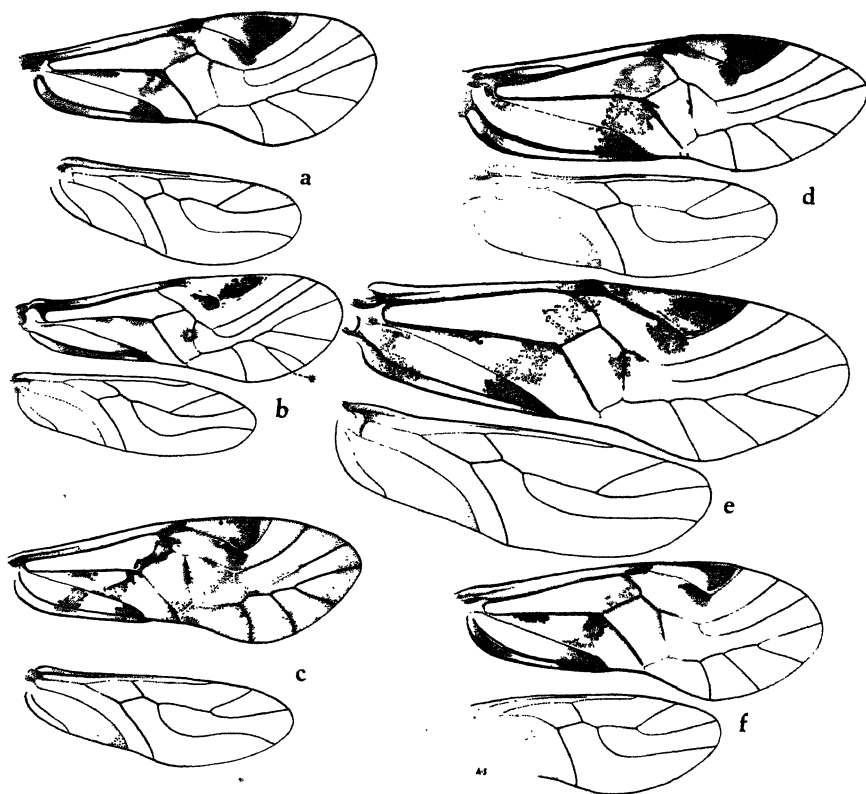


Figure 136—Wings of holotypes of *Psocus*: a, *P. lanaiensis* Perkins, male; b, *P. molokaiensis* Perkins, male (vein marked by asterisk is not forked in left wing); c, *P. monticola* Perkins, male; d, *P. oahuensis* Perkins, female; e, *P. simulator* Perkins, male; f, *P. sylvestris* Perkins, male. (Drawn at the British Museum of Natural History by Smith.)

Psocus oahuensis Perkins (fig. 136, d).

Psocus oahuensis Perkins, 1899:81.

Clematostigma distinguendum oahuensis (Perkins) Enderlein, 1913:355.

Endemic. Oahu (type locality: Waianae Mountains).

Hostplants: *Acacia koa*, *Pipturus*, *Neowawraea*.

Psocus simulator Perkins (fig. 136, e).

Psocus simulator Perkins, 1899:78.

Clematostigma simulator (Perkins) Enderlein, 1913:355.

Endemic. Maui (type locality: Mount Haleakala, 5,000 feet, October, 1896).

Psocus sylvestris Perkins (fig. 136, f).

Psocus sylvestris Perkins, 1899:81.

Clematostigma sylvestris (Perkins) Enderlein, 1913:355.

Endemic. Hawaii (type locality: Kona, 4,000 feet, 1892).

Hostplant: *Myoporum*.

This species was labeled *Psocus immaturus* Perkins in the *Fauna Hawaiiensis* collection: the type also bears the same name label.

Psocus unicus Perkins (fig. 137, a).

Psocus unicus Perkins, 1899:78.

Clematostigma unicus (Perkins) Enderlein, 1913:355.

Endemic. Maui (type locality: Mount Haleakala, 5,000 feet, May, 1896), Hawaii.

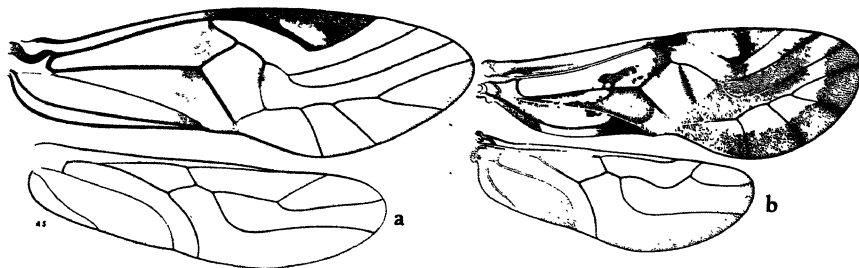


Figure 137—Wings of *Psocus*: a, *P. unicus* Perkins, holotype; b, *P. vittipennis* Perkins, holotype female. (Drawn at the British Museum of Natural History by Smith.)

Psocus vittipennis Perkins (fig. 137, b).

Psocus vittipennis Perkins, 1899:82.

Clematostigma vittipennis (Perkins) Enderlein, 1913:355.

Endemic. Kauai (type locality: Waimea Mountains, 4,000 feet, 1894).

The following is a synopsis of Enderlein's arrangement of the "species" of Perkins. I have not repeated the *Fauna Hawaiiensis* references, the synonymy involving *Clematostigma* or the locality data which have been given in detail above.

Psocus distinguendus Perkins. Enderlein, 1920:452, fig. 7.

Psocus distinguendus variety **oahuensis** (Perkins) Enderlein, 1920:452.

Psocus distinguendus variety **vittipennis** (Perkins) Enderlein, 1920:453.

Psocus haleakalae Perkins. Enderlein, 1920:449, fig. 1.

Psocus unicus Perkins; synonymy by Enderlein, 1920:449.

Psocus haleakalae variety **hualalai** (Perkins) Enderlein, 1920:451, fig. 4.

Psocus simulator Perkins; synonymy by Enderlein, 1920:451.

Psocus haleakalae variety **lanaiensis** (Perkins) Enderlein, 1920:450.

Psocus sylvestris Perkins; synonymy by Enderlein, 1920:451, fig. 3.

Psocus heterogamias Perkins; synonymy by Enderlein, 1920:451.

Psocus haleakalae variety **molokaiensis** (Perkins) Enderlein, 1920:451, fig. 5.

Psocus konae Perkins; synonymy by Enderlein, 1920:451.

Psocus kauaiensis Perkins; synonymy by Enderlein, 1920:451, fig. 6. Banks, 1931:437, considers this to be a good species.

Psocus haleakalae variety **monticola** (Perkins) Enderlein, 1920:450, fig. 2.

SPECIES INCERTAE SEDIS

The following species does not belong to the genus to which it was assigned, and in the absence of either specimen or illustration I am unable to place it.

(*Stenopsocus* ?) **pulchripennis** Perkins, 1899:83.

Endemic. Hawaii (type locality: Mount Hualalai, 8,000 feet).

Known only from the unique, mutilated holotype in the British Museum.

CORRODENTIA LITERATURE CONSULTED

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Order MALLOPHAGA Nitzsch, 1818

(*mallos*, lock of wool; *phagein*, to eat)

Aptera Linnaeus, 1758, in part.

Parasita Latreille, 1802, in part.

Anoplura, family *Nirmides* Leach, 1815.

Mallophaga Nitzsch, 1818.

Mandibulata Latreille, 1825.

Lipoptera Shipley, 1904.

Biting Lice

Body elongate to rotund, depressed, soft, integument tough. Head large, exposed, usually broader than prothorax, porrect; mouth parts on underside, fitted for biting; labrum well developed; mandibles large, tridentate; maxillae with single lobes, maxillary "rods" present in some forms, palpi four-segmented or absent; labium with greatly reduced or obsolete palpi; anterior part of oesophagus sclerotized to form the "oesophageal sclerite"; hypopharynx complex, well developed, most forms with associated "rod-like stalks"; antennae three-, four- or five-segmented, shorter than head; eyes reduced; ocelli absent. Thorax with prothorax usually free, but meso- and metathorax united or separated by a suture; with one pair of ventral prothoracic spiracles. Wings or wing rudiments absent. Legs with one- or two-segmented tarsi; tarsi usually with paired claws, but there may be one pair or none. Abdomen apparently nine-segmented in the adult; cerci absent; spiracles on segments three to eight, two to seven or three to seven; male genitalia large, usually with strongly sclerotized parts; female without an ovipositor, vaginal orifice situated behind ventrite seven. Metamorphosis incomplete; eggs cemented singly to feathers or hairs of host; four instars. Non-bloodsucking, ectoparasites of birds and mammals, but principally on birds. Size range from 0.5 mm. to 10.0 mm.

There are more than 2,000 species of biting lice described from all parts of the world. No fossil forms are known.

In contrast to the Anoplura, the members of the Mallophaga do not suck blood, and none is a parasite of man. By far the greatest numbers are ectoparasites of birds. The food of this group of lice consists principally of feathers, dead skin and hair of the host. The injury done by biting lice is largely the result of severe surface irritation. Heavy infestations are known to cause the death of certain hosts. Severe injury can also be done to the feathers, hair or wool of the host. It has been thought that biting lice did not feed upon blood, but studies by Crutchfield and Hixson (1943) show that at least some lice take blood meals regularly. They say (1943:66):

Barbs and barbules of feathers and blood comprise the food of the chicken body louse (*Menacanthus stramineus*) and a species of *Menacanthus* unrecognized, heretofore, as a pest of poultry in the United States. These species obtain blood by gnawing through the epidermis of the skin and rupturing the quills of pinfeathers. The diet of the shaft louse (*Menopon gallinae*) consists of barbs and barbules. The wing louse (*Lipeurus caponis*) feeds on hooklets of the flight feathers; occasionally, barbs and barbules form a part of the diet. The large chicken louse (*Goniocotes gigas*) and the fluff louse, (*Goniocotes hologaster*) feed largely on barbs and to some extent on barbules.

Clay and Meinertzhagen (1943) have summarized the data concerning the transportation of lice from one host to another through the agency of hippoboscids flies. The lice attach themselves to the flies and may be transferred to abnormal hosts. Some lice are able to escape from dead hosts by riding on the flies when they quit the cold host.

This order has received little attention in Hawaii. The only extensive paper on our species is the partial report of Kellogg and Chapman (1902, reprinted 1904; the types of the species described from Hawaii in that paper should be at Stanford University). There has never been an over-all survey. Only one species was recorded from domestic fowl prior to 1927. Perhaps some light could be thrown upon the drepaniid bird problem if an adequate number of species of lice from that avian family were available for study. It is a pity that the lice collected from the native birds by Perkins were not worked up. (See discussion under Mallophaga in chapter 3 of volume 1 for additional comment.)

Lice can be collected easily if birds and mammals are wrapped completely in cotton as soon as killed. The lice on the animals will leave the cold, dead bodies and migrate into the cotton where they will become trapped and die and may later be picked out. The cotton wrapping from each animal may be placed in a paper bag on which data are written and stored for future study by a louse specialist. Bird collectors should keep this in mind.

The hosts listed hereinafter are those reported for Hawaii only, and I have not made a general listing of the hosts of the various species listed from without the islands. A number of the local host records are obviously from straggler specimens—possibly having been transferred from one host to another in collectors' bags.

I have had much difficulty in writing the following outline, not only because of the confused state of mallophagan taxonomy and the lack of certain literature, but because there has been no adequate collection of lice available for study. I have seen Hawaiian specimens of only a few of the commonest species listed. This is probably the most unsatisfactory chapter in this book.

Miss Theresa Clay has given some constructive criticism and has aided me with the text in several places. Dr. E. W. Stafford has been especially helpful with the Philopteridae; his aid in the construction of the key to the genera and his notes on the generic position of various species have been particularly useful in strengthening the work.

TABULAR ANALYSIS OF THE HAWAIIAN MALLOPHAGA

FAMILY	GENERA	ENDEMIC GENERA	NON- ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	INDI- GENOUS SPECIES	ADVENTIVE SPECIES
Gyropidae	2	0	2	2	0	0	2
Boopiidae	1	0	1	1	0	0	1
Menoponidae	7	0	7	14	3	5	6
Trichodectidae	3	0	3	5	0	0	5
Philopteridae	19	0	19	30	2(?)	12	16
Totals	32	0	32	52	5(?)	17	30

Percentage of endemism in native group: genera 0 percent; species 28 percent (?).

Percentage of present-day fauna native: 43 percent.

Percentage of present-day fauna adventive: 57 percent.

Average number of species per genus in native group: 1.5.

Average number of species per genus in adventive group: 1.4.

This group is so poorly known that these figures may not be very accurate. Bird lice are generally widespread insects, and this is especially true of those attached to the widely wandering sea and shore birds; such a large percentage of indigenous species is not found in other orders of Hawaiian insects.

KEY TO THE SERIES OF MALLOPHAGA

1. Antennae clavate or capitate, four- or five-segmented, concealed in ventro-cephalic scrobes; maxillary palpi present, two-, three-, four- or five-segmented; line of division between meso- and metathorax usually distinct.....**Amblycera.**
2. Antennae filiform or seriform, three- or five-segmented, not concealed in ventral scrobes, but normally visible and extended; maxillary palpi absent; meso- and metathorax always fused with dividing suture obsolete.....**Ichnocera.**

Series AMBLYCERA (Kellogg, 1896)

KEY TO THE FAMILIES OF AMBLYCERA FOUND IN HAWAII

1. Mid and hind tarsi each with a single claw, or tarsal claws absent; our species on guinea pigs.....**Gyropidae.**
Tarsal claws paired; not ectoparasites of guinea pigs..... 2
2. Antennae five-segmented; body hairs mostly stiff and spiniform; ectoparasites of marsupials and dogs; male genitalia with accessory sac**Boopiidae.**
Antennae four-segmented; body hairs fine; ectoparasites of birds; male genitalia without accessory sac.....**Menoponidae.**

Family GYROPIDAE Kellogg, 1908

The Biting Guinea Pig Lice

This family is endemic to America (principally South America), but a few of the species have become widespread because of the activities of man. Almost all the species of the family (which totaled about 30 in 1924) are restricted to rodents, and only a few species have been found on primates, ungulates and on a sloth.

The eggs of the two species recorded hereafter are laid singly at the bases of the hair on guinea pigs. Ewing (1924:3) said that "The food of both these species consists in part of cutaneous secretions and excretions and in the case of *G. porcelli* of serum in addition. . . ." Sodium fluoride or a 2 to 5 percent rotenone dust is suggested to control these lice.

KEY TO THE SUBFAMILIES AND GENERA OF GYROPIDAE FOUND IN HAWAII

1. Short, broad species; maxillary palpi four-segmented; tarsal claws developed; meso- and metathoracic legs with femora fitted with a forked and grooved tenaculum for reception of tarsus when closed into it; tarsus with segment two elongate, transversely furrowed. **Gyropus** of the Gyropinae.
2. Slender species; maxillary palpi two-segmented; tarsi greatly reduced, claws absent; meso- and metathoracic legs with femora and tibiae arcuate and transversely striate.
 **Gliricola** of the Gliricolinae.

Subfamily GYROPINAE Ewing, 1924:9

Genus **GYROPUS** Nitzsch, 1818**Gyropus ovalis** Nitzsch.

Gyropus ovalis Nitzsch, 1818:304 (I have not confirmed this reference). Ewing, 1924:13, fig. 6. Genotype.

The oval guinea pig louse.

Oahu.

Immigrant. Not recorded heretofore, but I took it in Honolulu in 1944. It is normally found on guinea pigs wherever the host is taken by man.

Host: guinea pig.

Subfamily GLIRICOLINAE Ewing, 1924:29

Genus **GLIRICOLA** Mjoeberg, 1910**Gliricola porcelli** (Linnaeus).

Pediculus porcelli Linnaeus, 1758:611. Ewing, 1924:33, figs. 15, 17; pl. 1, fig. 8.

Oahu (and probably on some of the other islands).

Immigrant. Widespread from South America by man. First found by me in Honolulu in 1943 (1944:200).

Host: guinea pig.

Family BOOPIIDAE Mjoeberg, 1910

The Biting Kangaroo Lice

This family is endemic to Australia where its species are ectoparasites of marsupials, with the exception of the species listed below. One species represents the family in Hawaii, and, because it is a parasite of dogs, it has been widely spread artificially. No search has been made for lice on the wallabies and kangaroos introduced into Hawaii, and perhaps other members of this louse family are also established in the Territory.

Subfamily BOOPIINAE Harrison and Johnson, 1916:345

Genus **HETERODOXUS** Le Souëf and Bullen, 1902

Paine, 1912:359, figs. *a-g*, note.

Heterodoxus spiniger (Enderlein).

Menopon spiniger Enderlein, 1909:80, figured.

Heterodoxus longitarsus, of authors, as recorded from dogs.

Oahu (and other islands?).

Immigrant. Widespread; described from South Africa. First recorded from Hawaii by Carpenter in Honolulu in 1933.

Host: dog.

In some regions, this louse is considered a serious pest of dogs and is so abundant as to cause the death of its canine hosts. It has not, to my knowledge, caused much trouble in Hawaii. It has been referred to as *Heterodoxus longitarsus* (Piaget, 1880:504, pl. 41, figs. 7, 7*a-c*), the kangaroo louse, but Werneck (1941:46) has shown that it is distinct.

Control: A dust made from one part sodium fluoride powder and three to five parts ordinary wheat flour by weight, or equal parts powdered derris and flour rubbed thoroughly into the fur is recommended. A 2 to 5 percent rotenone dust may also be useful.

Family MENOPONIDAE Mjoeberg, 1910

KEY TO THE SUBFAMILIES

1. Prothorax much smaller than head; lateral margins of temples rounded **Menoponinae.**
2. Prothorax very large, about as large as head; temples angulate **Ancistroninae.**

Subfamily MENOPONINAE

KEY TO THE GENERA FOUND IN HAWAII

1. Ventral side of posterior femora without a condensed patch of setae; second, third, or fourth abdominal sternites without patches of setae or asters of heavy spines. **Colpocephalum** Nitzsch.
- Ventral side of posterior femora with a condensed patch of setae; second, third or fourth abdominal sternites with a condensed patch of setae and/or an aster of heavy spines on either side 2
- 2(1). Lateral margin of head with a deep emargination just before the eye (ocular emargination) **Actornithophilus** Ferris.
- Lateral margins of head not so emarginate, continuous to eye, but a slit or fracture is present in front of eyes in *Menopon* 3
- 3(2). Ventral surface of head with a sclerotized, hook-like process near base of each mandible. **Eomenacanthus** Uchida.
- Without such processes 4
- 4(3). Forehead with a fracture-like slit in margin near eyes; oesophageal sclerites heavily sclerotized. **Menopon** Nitzsch.
- Forehead without such a marginal slit. 5
- 5(4). Second abdominal ventrite with asters of spines; without a conspicuous gular plate. **Myrsidea** Waterston.
- Second abdominal ventrite without asters of spines; gular plate conspicuously pigmented. **Machaerilaemus** Harrison.

Genus **EOMENACANTHUS** Uchida, 1926:30

Eomenacanthus stramineus (Nitzsch) (fig. 138).

Liotheum (*Menopon*) *stramineum* Nitzsch, 1818:300; 1874:291.

Menopon biseriatum Piaget, 1880:469, pl. 37, fig. 2.

Eomenacanthus biseriatum (Piaget) Uchida, 1926:31.

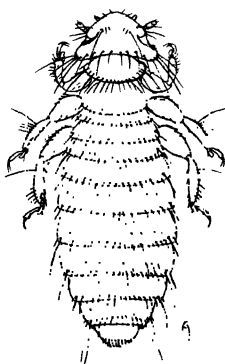


Figure 138—*Eomenacanthus stramineus* (Nitzsch), the chicken body louse. (Abernathy drawing.)

The chicken body louse; Hawaiian name: "‘uku-moa."

Oahu, Molokai, Hawaii.

Immigrant. Cosmopolitan. First recorded from Hawaii by Illingworth from specimens collected on Oahu in 1926.

Hosts: chicken, California valley quail (recorded elsewhere also on turkey, guinea hen and pigeon).

I have records only from Oahu, Molokai and Hawaii, but I assume that it is present on the other islands.

Control may be obtained by the use of sodium fluoride or pyrethrum dusts.

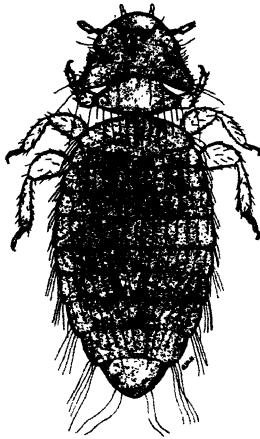


Figure 139—*Menopon gallinae* (Linnaeus), the common hen louse. (After Herrick, 1915.)

Genus **MENOPON** Nitzsch, 1818

Menopon gallinae (Linnaeus) (fig. 139).

Pediculus Gallinae Linnaeus, 1758:613.

Menopon pallidum Nitzsch, 1874:291.

The common hen louse; Hawaiian name: "‘uku-moa."

Kauai, Oahu. Not recorded from the other islands, but certainly present on poultry throughout the Territory.

Immigrant. Cosmopolitan. First recorded from Hawaii by Illingworth in 1928, but established here much earlier.

Hosts: chicken, duck, guinea hen, pigeon, turkey.

Sodium fluoride dusts give good control.

Menopon phaeostomum Nitzsch.

Menopon phaeostomum Nitzsch, 1866:391.

Oahu.

Immigrant. Cosmopolitan. First collected in the Territory by Illingworth in 1926 at Honolulu.

Hosts: guinea hen and peafowl.

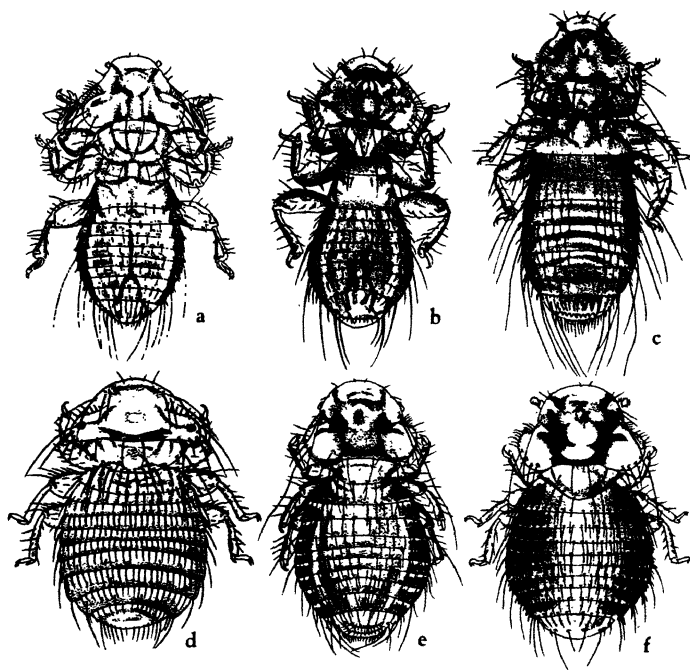


Figure 140—Hawaiian bird lice: a, *Myrsidea conspicua* (Kellogg and Chapman), male; b, *Myrsidea cyrtostigma* (Kellogg and Chapman), male; c, *Myrsidea invadens* (Kellogg and Chapman), female; d, *Machaerilaemus hawaiiensis* (Kellogg and Chapman), female; e, *Colpocephalum brachysomum* Kellogg and Chapman, female; f, *Colpocephalum discrepans* Kellogg and Chapman, female. (Rearranged from Kellogg and Chapman, 1904.)

Genus **MYRSIDEA** Waterston, 1915

Myrsidea conspicua (Kellogg and Chapman) (fig. 140, a).

Colpocephalum conspicuum Kellogg and Chapman, 1902:163, pl. 14, fig. 4; 1904:315, pl. 10, fig. 9.

Myrsidea conspicua (Kellogg and Chapman) Ferris, 1916:308.

Maui (type material from Kahului and "Pau [?] Olai").

Immigrant (from America?).

Host: *Carpodacus mexicanus obscurus* (house finch).

This species has thus far only been recorded from Maui, but, because it was taken from an introduced bird, I presume that it is most certainly an immigrant species. When the lice are better known, this species will probably prove to be a synonym of some American louse.

Myrsidea cyrtostigma (Kellogg and Chapman) (fig. 140, b).

Menopon cyrtostigmum Kellogg and Chapman, 1902:165, pl. 15, fig. 3; 1904:318, pl. 10, fig. 12.

Myrsidea cyrtostigma (Kellogg and Chapman) Ferris, 1916:308.

Endemic. Maui, Hawaii (type material from both islands).

Hosts: *Chlorodrepanis virens* ("amakihi"), *Himatione sanguinea* ("apapane"), *Ictiaria coccinea* ("iiwi"). All these recorded hosts are endemic Hawaiian birds (Drepaniidae).

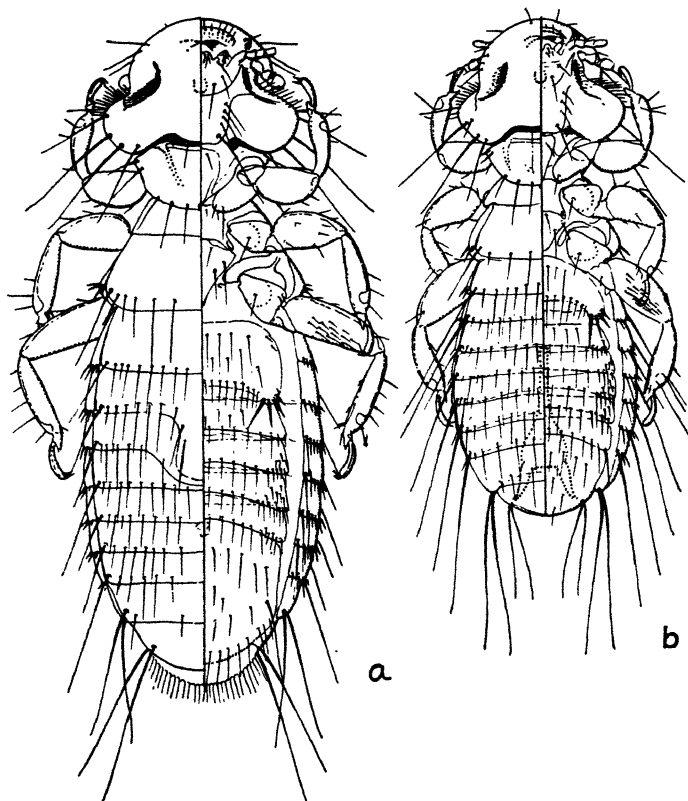


Figure 141—*Myrsidea invadens* (Kellogg and Chapman): a, female; b, male. (After Ferris, 1932:10.)

Myrsidea invadens (Kellogg and Chapman) (fig. 140, c; 141, a-b).

Menopon invadens Kellogg and Chapman, 1902:167, pl. 15, fig. 5; 1904:320, pl. 10, fig. 14.

Myrsidea invadens (Kellogg and Chapman) Ferris, 1916:308; 1932:10, figs. 3, 4.

Molokai, Maui (type locality: Maui).

Immigrant. Recorded from the mynah at Tahiti by Ferris in 1932, but certainly with a much wider distribution, although it is unrecorded elsewhere.

Hosts: *Acridotheres tristis* (mynah). *Streptopelia* (*Spilopelia*, *Turtur*) *chinensis* (Chinese dove) (straggler ?).

I have seen records from Maui and Molokai only, but I assume that the species is found wherever the mynah bird is distributed about the islands, but it has not been searched for.

Genus **MACHAERILAEMUS** Harrison, 1915

Machaerilaemus hawaiiensis (Kellogg and Chapman) (fig. 140, d).

Menopon hawaiiensis Kellogg and Chapman, 1902:165, pl. 15, fig. 2; 1904:317, pl. 10, fig. 11.

Endemic. Maui (type locality: Iao Valley).

Host: *Chlorodrepanis virens* (native drepaniid "amakihi").

Genus **COLPOCEPHALUM** Nitzsch, 1818

Colpocephalum brachysomum Kellogg and Chapman (fig. 140, e).

Colpocephalum brachysomum Kellogg and Chapman, 1902:162, pl. 14, fig. 3; 1904:314, pl. 10, fig. 8.

Indigenous (?). Maui (type series from Kahului and Iao Valley).

Hosts: *Asio flammeus sandwichensis* (*Asio accipitrinus*) (the Hawaiian owl), and *Pluvialis dominica fulva* (*Charadrius dominicus fulvus*) (Pacific golden plover). Thompson (1938:206) believes that *Asio* is the true host.

Colpocephalum discrepans Kellogg and Chapman (fig. 140, f).

Colpocephalum discrepans Kellogg and Chapman, 1902:164, pl. 14, fig. 1; 1904:316, pl. 10, fig. 10.

Indigenous. Maui (type locality: Kahului).

Hosts: *Anous stolidus pileatus* (noddy tern), *Carpodacus mexicanus obscurus* (house finch or linnet).

Colpocephalum hilensis (Kellogg and Chapman) (fig. 145, a).

Menopon hilensis Kellogg and Chapman, 1902:166, pl. 15, fig. 4; 1904:319, pl. 10, fig. 13.

Endemic. Hawaii (type locality: Hilo).

Host: *Vestiaria coccinea* (the beautiful black and red native drepaniid "iwi").

Colpocephalum turbinatum Denny.

Colpocephalum turbinatum Denny, 1842:209.

Oahu.

Immigrant. A widespread species. First found in Hawaii in 1945 by members of the armed forces, but not recorded in Hawaiian literature heretofore.

Host: pigeon.

Genus **ACTORNITHOPHILUS** Ferris, 1916:303

Actornithophilus epiphanes (Kellogg and Chapman) (fig. 145, b).

Colpocephalum epiphanes Kellogg and Chapman, 1902:161, pl. 14, fig. 2; 1904:313, pl. 10, fig. 7.

Actornithophilus epiphanes (Kellogg and Chapman) Ferris, 1916:304.

Indigenous. Maui (type locality: Kahului).

Host: *Anous stolidus pileatus* (noddy tern).

Actornithophilus kilauensis (Kellogg and Chapman) (fig. 145, c).

Colpocephalum kilauensis Kellogg and Chapman, 1902:161, pl. 14, fig. 1; 1904:312, pl. 10, fig. 6.

Actornithophilus kilauensis (Kellogg and Chapman) Ferris, 1916:304.

Indigenous. Hawaii (type locality: Hilo).

Host: *Heterocelus* (*Heteractitis*) *incanus* (wandering tattler).

Subfamily ANCISTRONINAE

Genus **ANCISTRONA** Westwood, 1874

Ancistrona vagelli (Fabricius).

Pediculus vagelli Fabricius, 1787:369.

Ancistrona gigas Piaget, 1883:152, pl. 9, fig. 1.

The giant bird louse.

Laysan.

Indigenous. Widespread about the world. First recorded from the Territory by Kellogg and Paine (1910:125).

Host: *Pterodroma leucoptera hypoleuca* (*Acstrelata hypoleuca*) (Bonin Island petrel).

Essig (1929:130) says that this is the broadest known louse.

Series ISCHNOCERA (Kellogg, 1896)

KEY TO THE FAMILIES OF ISCHNOCERA FOUND IN HAWAII

1. Tarsi with single claws; antennae three-segmented (at least in male); ectoparasites of mammals. **Trichodectidae.**
2. Tarsi with paired claws; antennae five-segmented; ectoparasites of birds **Philopteridae.**

Family TRICHODECTIDAE Kellogg, 1908

This family contains a number of pests which are of major economic importance elsewhere, but they have caused little concern in Hawaii.

KEY TO THE GENERA OF TRICHODECTIDAE FOUND IN HAWAII

1. Forehead triangular, almost straight on sides; with fewer than six abdominal spiracles; ectoparasites on cats. . . . **Felicola** Ewing.
Forehead rounded, broader than long; with six abdominal spiracles; not found on cats. 2
2. Ectoparasites of goats, sheep, cattle and horses; parameres of male genitalia free; antennae of male and female similar; forehead without hair-groove. **Bovicola** Ewing.
Ectoparasites of dogs; parameres of male genitalia united distally; antennae of male and female dissimilar; hair-groove present on forehead. **Trichodectes** Nitzsch.

Genus **TRICHODECTES** Nitzsch, 1818

According to Ewing (1929:121), this genus includes, in its restricted sense, those species of the family which have the "antennae three segmented in both sexes but of different shape; temporal lobes without posterior processes; forehead rounded; all of the abdominal segments with pleural plates."

Trichodectes canis (Degeer).

Ricinus canis Degeer, 1778:81, pl. 4, fig. 16.

Trichodectes latus Nitzsch, 1838:436. Piaget, 1880:384, pl. 31, fig. 6.

The biting dog louse.

Oahu. Not recorded from the other islands; probably present on all of the main islands, but not yet searched for.

Immigrant. Cosmopolitan. First recorded from Hawaii by Swezey from specimens taken in Honolulu in 1929, but no doubt here at an early date.

Host: dog.

This species has apparently not caused much concern to keepers of dogs in the Territory, for it has been infrequently called to the attention of local entomologists. However, in other localities, severe infestations, especially in young animals, have been reported.

Control: sodium fluoride dusts are effective.

In the late 1860's, Melnikoff and Leuckart found that this louse served as an intermediate host for the common double-pored dog tapeworm, *Dipylidium caninum* (Linnaeus). This discovery is said to be the first to show that an arthropod was involved as an intermediate host of a parasitic worm. The tapeworm is common in dogs and cats and occasionally is recorded from human beings. Most of the human cases have been young children. Human infestation occurs by ingesting an infested louse or flea or crushed parts of these insects. Putting one's fingers in one's mouth after crushing a louse or flea, or handling a pet or allowing a dog, which may have bitten a louse or a flea, to lick one are routes of possible infection. The eggs of the tapeworm are expelled with the host's feces and those which become lodged on the hair or body of the dog or cat may be ingested by the lice. When the tapeworm eggs reach the intestines of the louse, they hatch, and the larval tapeworms bore through the intestines and develop into the cystocercoid stage in the body cavity of the louse. When the cystocercoid stage is reached, the tapeworms are capable of infesting their mammalian hosts. The mature tapeworm reaches a length of about 12 inches. Its mature proglottids are sub-ovate or pumpkin-seed-shaped and have a double reproductive system with a genital pore at about the middle of each side—hence the name double-pored tapeworm.

Genus **BOVICOLA** Ewing, 1929:123

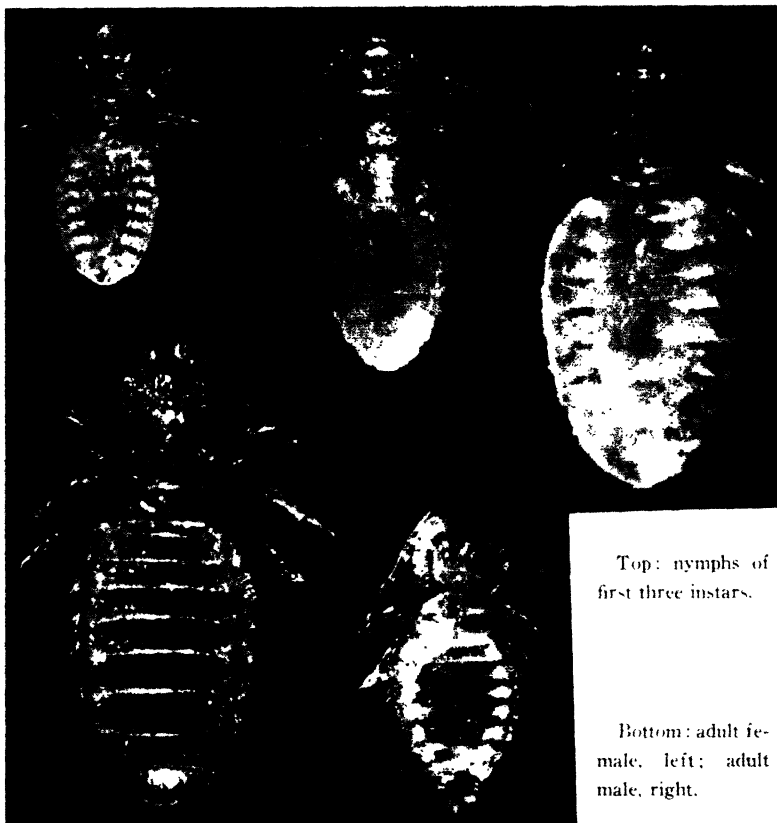
This genus can be readily distinguished from *Felicola* because of the shape of its forehead, which is rounded and much broader than long. It was separated from *Trichodectes* principally because the antennae of the males and females are similarly shaped and the shape of the head is different.



Figure 142—Egg of *Bovicola bovis* (Linnaeus) on a cattle hair. (Photograph kindly furnished by J. G. Matthyse.)

KEY TO THE SPECIES OF BOVICOLA FOUND IN HAWAII

1. Ectoparasitic on cattle **bovis** (Linnaeus).
2. Ectoparasitic on goats **caprae** (Gurlt).
3. Ectoparasitic on horses **equi** (Linnaeus).
4. Ectoparasitic on sheep **ovis** (Linnaeus).



Top: nymphs of first three instars.

Bottom: adult female, left; adult male, right.

Figure 143—*Bovicola bovis* (Linnaeus), the biting ox louse. (I am indebted to Dr. J. G. Matthyse for supplying the photographs for this plate.)

Bovicola bovis (Linnaeus) (figs. 142, 143).

Pediculus Bovis Linnaeus, 1758:611.

Trichodectes scalaris Nitzsch, 1818:269 (I have not checked this reference).

The biting ox louse; the cattle red louse.

Molokai, and probably all of the main islands.

Immigrant. Cosmopolitan. First found in Hawaii in 1943 by me on a cow from Molokai examined in Honolulu.

Control: the same as for the biting horse louse, as outlined below. Raw (not boiled) linseed oil applied with a brush is also a good and cheap method of control (keep the treated animal quiet and under cover for at least 12 hours after treatment).

It appears that this species usually reproduces parthenogenetically, but males are known to occur. It is found most abundantly on the back of the host from the neck to the base of the tail. High temperature and high humidity are unfavorable for the development of the louse.

"The instars can readily be distinguished by both head capsule measurements and morphological characters. The first instar nymphs are completely light colored, unchitinized, along the lateral margins of the abdomen. In the second instar the lateral margins of the first visible abdominal segment are partly chitinized, brownish. In the third instar the first visible segment is completely chitinized along the lateral margin, the second segment also partly chitinized, brownish." (Matthysse, 1944:439.)

***Bovicola caprae* (Gurlt).**

Trichodectes caprae Gurlt, 1842:3, pl. 1, fig. 2.

Trichodectes climax Nitzsch, 1818:296.

Bovicola caprae (Gurlt) Ewing, 1929:123. Genotype.

The biting goat louse.

Oahu, and probably all of the main islands.

Immigrant. Cosmopolitan. I have seen specimens collected in Honolulu in 1920, and these were recorded by me in 1943 (1944:200).

Host: goat.

***Bovicola equi* (Linnaeus).**

Pediculus Equi Linnaeus, 1758:612.

Trichodectes equi (Linnaeus), of authors.

Bovicola equi (Linnaeus) Ewing, 1929:123.

The biting horse louse.

Oahu (and the other main islands?).

Immigrant. Cosmopolitan. Not heretofore recorded from Hawaii, but reported to me as being present on army horses at Schofield Barracks in 1943.

Host: horse.

Control: local infestations may be controlled by sodium fluoride dusts, but if infestations are heavy and extensive the following standard dip solution has been recommended: white arsenic, 4 pounds; sal soda, 12 pounds; pine tar, 2 quarts; water, 250 gallons. The recently developed DDT dusts and sprays will probably replace the older control methods.

Bovicola ovis (Linnaeus).

Pediculus Ovis Linnaeus, 1758:611.

Trichodectes ovis (Linnaeus), of authors.

Bovicola ovis (Linnaeus) Ewing, 1929:123.

The biting sheep louse.

This cosmopolitan species has not been reported in literature from Hawaii, but circumstantial evidence leads me to believe that it will be found, especially on the island of Hawaii, if searched for. In some mainland localities when active dipping for sheep scab is not carried on, it is said that these lice build up occasionally in troublesome numbers, but that the usual dipping of the flocks keeps the louse under control.

Genus FELICOLA Ewing, 1929:122, 192

This genus can be recognized among the other Trichodectidae most easily because of its anteriorly pointed head.

Felicola subrostrata (Nitzsch).

Trichodectes subrostrata Nitzsch, 1818:296.

Felicola subrostrata (Nitzsch) Ewing, 1929:122. Genotype.

The biting cat louse.

Oahu, and probably on the other islands.

Immigrant. Cosmopolitan. This species was first recorded by me from specimens from Honolulu in 1943 (1944:200), but it has been here for a long while.

It is said that cats may become heavily infested with this louse, but no records of severe infestation in the Territory have come to my attention.

Control: sodium fluoride diluted in three or four parts of flour gives good control and will not irritate the cat's tender skin as will straight sodium fluoride.

Family PHILOPTERIDAE Burmeister, 1838**The Biting Bird Lice**

This is the largest family of lice. All our species can be distinguished easily from the only other family of lice of the Ischnocera found in Hawaii because of their two-segmented tarsi and five-segmented antennae. This family is in a state of taxonomic chaos. The following key is poor, but I am unable to improve it with the material and data at hand. It appears that some of these genera exist more in the minds of certain taxonomists than in nature.

KEY TO THE GENERA OF PHILOPTERIDAE FOUND IN HAWAII

1. Inner margin of each eighth abdominal pleuron of female with a process bearing one or more spines; head not broader than long, each temple with only one very long seta and not produced into processes nor angulate in our species, which is found on the Hawaiian coot.
 **Rallicola** Johnston and Harrison.
 Not such species 2
- 2(1). Forehead without a complete marginal band, rarely rounded; clypeal suture and signature usually present.... 3
 Forehead rounded and surrounded by a narrow, unbroken marginal band; usually without a clypeal suture or signature 12
- 3(2). Body elongate; trabecula small or absent..... 4
 Body rotund; trabecula usually large and movable..... 7
- 4(3). First three antennal segments of male distinctly elongated, especially second segment, and different from those of female; our species on albatrosses.....
 **Docophoroides** Giglioli.
 Not such species; antennae alike in the sexes..... 5
- 5(4). Clypeal region completely surrounded by a subcircular, hyaline margin; with a pair of small, peg-like, dorsal spines behind clypeal suture..... **Anotoecus** Cummings.
 Not such forms 6
- 6(5). Male genitalia with basal plate uniformly sclerotized; parameres short **Philopterus** Nitzsch.
 Male genitalia with only lateral margins of basal plate sclerotized; parameres long, heavy, saber-shaped.....
 **Saemundsson** Timmerman.
- 7(3). Antennae similar in the sexes..... 8
 First antennal segment of male larger and different from that of female, first and third segments may have appendages 9
- 8(7). Signature and clypeal suture absent; antennal bands interrupted medianly **Brüelia** Kéler.
 Signature and clypeal suture present.....
 **Quadriceps** Clay and Meinertzhagen.
- 9(7). Large species, 8 to 9 mm. long; signature broader than long; first antennal segment of male with an appendage **Harrisoniella** Bedford.
 Much smaller, 2 to 4 mm. long; signature not transverse; first segment of male antenna usually without an appendage 10
- 10(9). Clypeus armed with two pairs of small, stout spines, these lying near apex, anterior pair directed forward and slightly downward, posterior pair directed upward and slightly backward; on pigeons..... **Columbicola** Ewing.
 Clypeus without such spines in addition to usual fine setae; not characteristic of pigeons..... 11

Kellogg, 1896:96, pl. 4, fig. 1.

Philopterus dentatus (Scopoli), of authors.

The red duck louse.

This species has not been recorded from Hawaii, but because it is a common, widespread louse of ducks, both wild and domesticated, I presume that it will be found in the islands if searched for. "This species is easily recognizable by its conspicuously rounding, uncolored clypeus with colored signature, and on each side of it the triangularly-headed anterior projection of the antennal band." (Kellogg, 1896:96-97.)

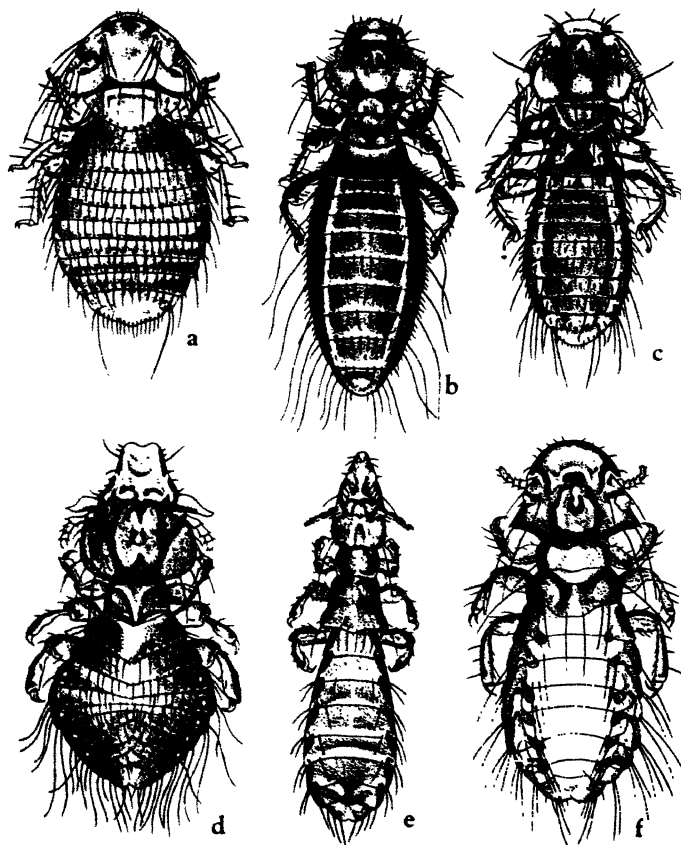


Figure 145—Some Hawaiian bird lice: a, *Colpocephalum hilensis* (Kellogg and Chapman), male; b, *Actornithophilus epiphanes* (Kellogg and Chapman), female; c, *Actornithophilus kilauensis* (Kellogg and Chapman), female; d, *Philopterus macgregori* (Kellogg and Chapman), female; e, *Brüelia stenozona* (Kellogg and Chapman), female; f, *Goniocotes chinensis* Kellogg and Chapman, female. (Rearranged from Kellogg and Chapman, 1904.)

Genus **DOCOPHOROIDES** Giglioli, 1864**Docophoroides brevis** (Dufour).

Philopterus Brevis Dufour, 1835:674, pl. 31, fig. 3.

Lipeurus taurus Nitzsch, 1866:385.

Eurymetopus taurus (Nitzsch) Taschenberg, Kellogg and Paine, 1910:125.

Kellogg, 1908:51, pl. 2, fig. 16.

Laysan.

Indigenous. Cosmopolitan. First recorded from the Territory from Laysan by Kellogg and Paine in 1910.

Hosts: *Diomedea nigripes* (black-footed albatross), *Diomedea (Thalassarche) immutabilis* (Laysan albatross).

Genus **SAEMUNDSSONIA** Timmerman, 1936:100**Saemundssonina conicus** (Denny).

Docophorus conicus Denny, 1842:90. pl. 5, fig. 2.

Docophorus fuliginosus Kellogg, 1896:80, pl. 3, fig. 2.

Docophorus fuliginosus variety *hawaiiensis* Kellogg and Chapman, 1902:157; 1904:307 (type series from Kahului, Maui, and Hilo, Hawaii).

Docophorus wallacei Johnston and Harrison, 1912:369, figs. 5, 6.

Philopterus conicus (Denny) Harrison, 1916:92.

Maui, Hawaii.

Indigenous. A widespread species. First recorded from Hawaii by Kellogg and Chapman in 1902.

Hosts: *Pluvialis (Charadrius) dominicus fulvus* (plover), *Heterocelus (Heteractitis) incanus* (wandering tattler).

Saemundssonina snyderi (Kellogg and Paine) (fig. 146, a-d).

Docophorus snyderi Kellogg and Paine, 1910:124, figs. 1, 2.

Philopterus snyderi (Kellogg and Paine) Harrison, 1916:104. Ferris, 1932:71, fig. 20, a-d.

Saemundssonina snyderi (Kellogg and Paine) Thompson, 1939:74.

Laysan (type locality).

Indigenous. Also known from the Marquesas Islands.

Hosts: *Sterna lunata* (gray-backed tern) in Hawaii, *Sterna fuscata* (sooty tern) in the Marquesas.

Ferris (1932:71) says that this species may be the same as the Galapagan *Saemundssonina (Philopterus) melanocephala* (Nitzsch).

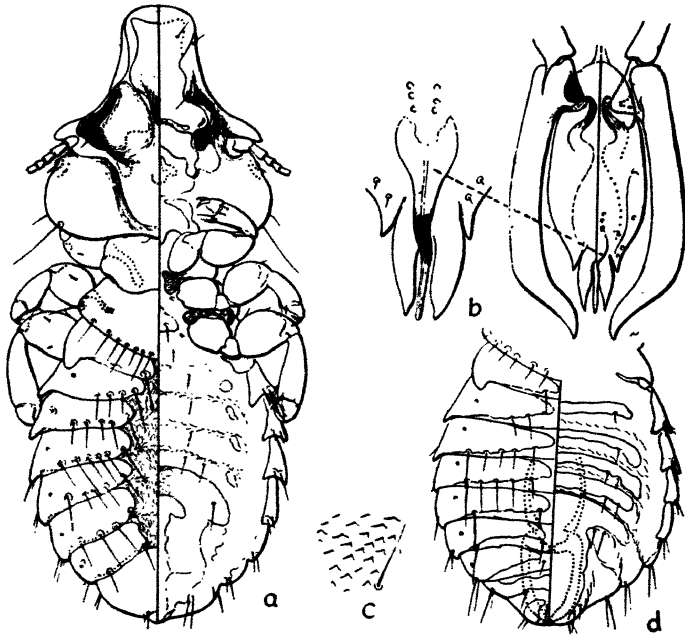


Figure 146—*Saemundssonina snyderi* (Kellogg and Paine): a, female; b, male genitalia; c, ornamentation of ventral surface of female; d, male abdomen, drawn to larger scale than female. (After Ferris, 1932:71.)

Genus **PHILOPTERUS** Nitzsch, 1818

Docophorus Nitzsch, 1818.

Philopterus macgregori (Kellogg and Chapman) (fig. 145, d).

Docophorus macgregori Kellogg and Chapman, 1902:156. pl. 13. fig. 1; 1904:306, pl. 10. fig. 1.

Endemic(?). Maui (type series from Kahului and Iao Valley).

Host: *Chlorodrepanis virens* ("amakihi").

Philopterus subflavescens (Geoffroy).

Pediculus subflavescens Geoffroy, 1762:599.

Docophorus communis Nitzsch, 1838:425.

Philopterus subflavescens (Geoffroy) Harrison, 1916:105.

Maui, Hawaii.

Immigrant. First recorded from Hawaii by Kellogg and Chapman in 1902. Known also from the Galapagos Islands.

Hosts in Hawaii: *Carpodacus mexicanus obscurus* (linnet); *Munia nisoria* (Chinese sparrow).

Genus **RALLICOLA** Johnston and Harrison, 1911

Rallicola advena (Kellogg).

Oncophorus advena Kellogg, 1896:133, pl. 11, figs. 1, 2. Kellogg and Chapman, 1902:160; 1904:311.

Rallicola advena (Kellogg) Harrison, 1916:126.

Maui, Hawaii.

Indigenous. Also found in California, where it was described from the American coot.

Hosts: *Fulica americana alai* (Hawaiian coot), *Vestiaria coccinea* ("iiwi"),

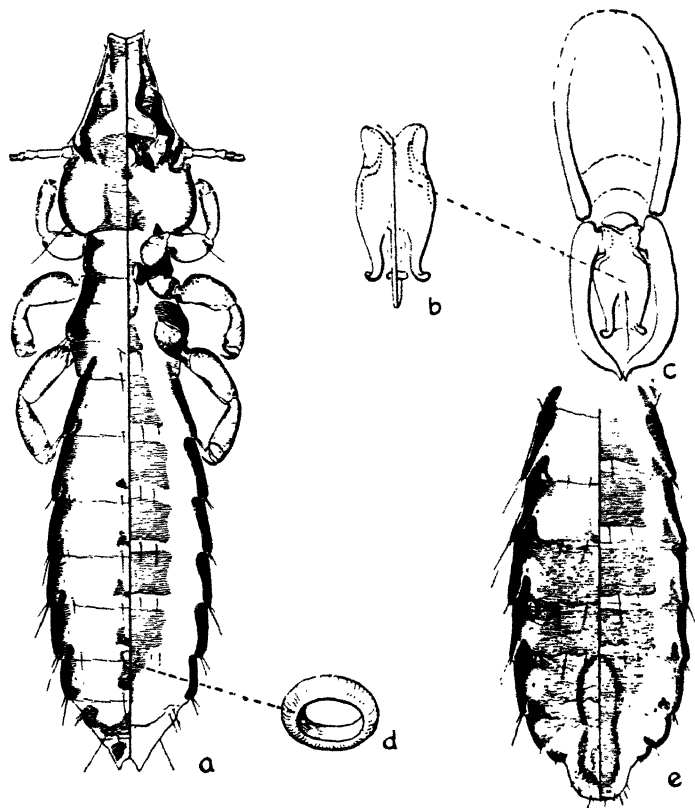


Figure 147—*Quadraceps birostris* (Giebel): a, female; b, endomer complex of male genitalia; c, male genitalia; d, spermatheca of female; e, abdomen of male, drawn to larger scale than female. (After Ferris, 1932:68.)

Heterocelus (*Heteractitis*) *incanus* (wandering tattler). These two latter records appear to be erroneous. Thompson (1939:122) believes that the coot is the true host.

Genus **QUADRACEPS** Clay and Meinertzhagen

Quadriceps birostris (Giebel) (fig. 147, a-e).

Nirmus birostris Giebel, 1874:174.

Nirmus gloriosus Kellogg and Kuwana, 1902:467, pl. 29, fig. 1, in part.

Degeeriella gloriosa (Kellogg and Kuwana) Harrison, 1916:114. Ferris, 1932: 68, fig. 18. a-e.

Degeeriella birostris (Giebel) Bedford, 1936:88.

Laysan.

Indigenous. Widespread. First recorded from Hawaii by Kellogg and Paine in 1910.

Host: *Sterna lunata* (gray-backed tern).

Quadriceps oraria (Kellogg).

Nirmus orarius Kellogg, 1896:104, pl. 5, fig. 104.

Nirmus orarius hawaiiensis Kellogg and Chapman, 1902:159; 1904:310 (type from Kahului, Maui).

Degeeriella oraria (Kellogg) Johnston and Harrison, 1912:368.

Maui.

Indigenous. Widespread. First recorded from the islands in 1902 by Kellogg and Chapman.

Hosts: *Pluvialis* (*Charadrius*) *dominicus fulvus* (plover), *Fulica americana alai* (Hawaiian coot). Thompson (1939:120) says that the plover is the true host.

Quadriceps separata (Kellogg and Kuwana) (fig. 148, a-e).

Nirmus separatus Kellogg and Kuwana, 1902:472, pl. 29, fig. 6.

Nirmus gloriosus Kellogg and Kuwana, 1902:467, pl. 29, fig. 1, in part, through misidentification.

Nirmus gloriosus variety *emarginatus* Kellogg and Chapman, 1902:159 (type from Kahului, Maui); 1904:310.

Degeeriella separata (Kellogg and Kuwana) Harrison, 1916:123. Ferris, 1932: 69, fig. 19, a-c.

Maui, Laysan.

Indigenous. Widespread. First recorded from the Territory by Kellogg and Chapman in 1902.

Host: *Anous stolidus pilcatus* (noddy tern).

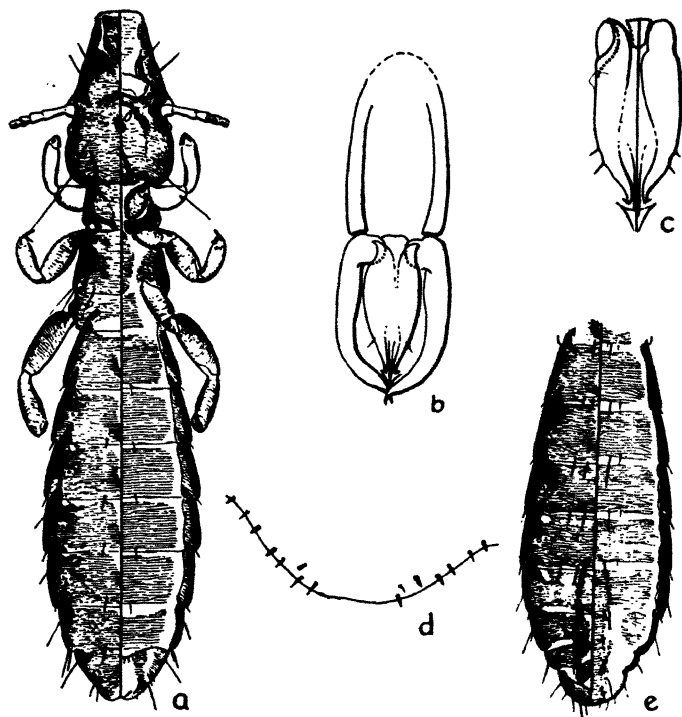


Figure 148—*Quadriceps separata* (Kellogg and Kuwana): a, female; b, male genitalia; c, endomeral complex of male genitalia; d, margin of vulva; e, abdomen of male, drawn to larger scale than female. (After Ferris, 1932:70.)

Genus **BRÜELIA** Kéler, 1936

Brüelia stenozona (Kellogg and Chapman) (fig. 145, e).

Nirmus stenozonus Kellogg and Chapman, 1902:158, pl. 13, fig. 3; 1904:308, pl. 10, fig. 3.

Degeeriella stenozona (Kellogg and Chapman), of authors.

Immigrant(?). Hawaii (type locality: Hilo).

Hosts: *Vestiaria coccinea* ("iwi"), *Munia nisoria* (Chinese sparrow).

Brüelia vulgata (Kellogg).

Nirmus vulgatus Kellogg, 1896:496, pl. 47, fig. 5.

Degeeriella vulgata (Kellogg), of authors.

Oahu, Gardner Island.

Immigrant. Widespread.

Host: *Passer domesticus* (English sparrow).

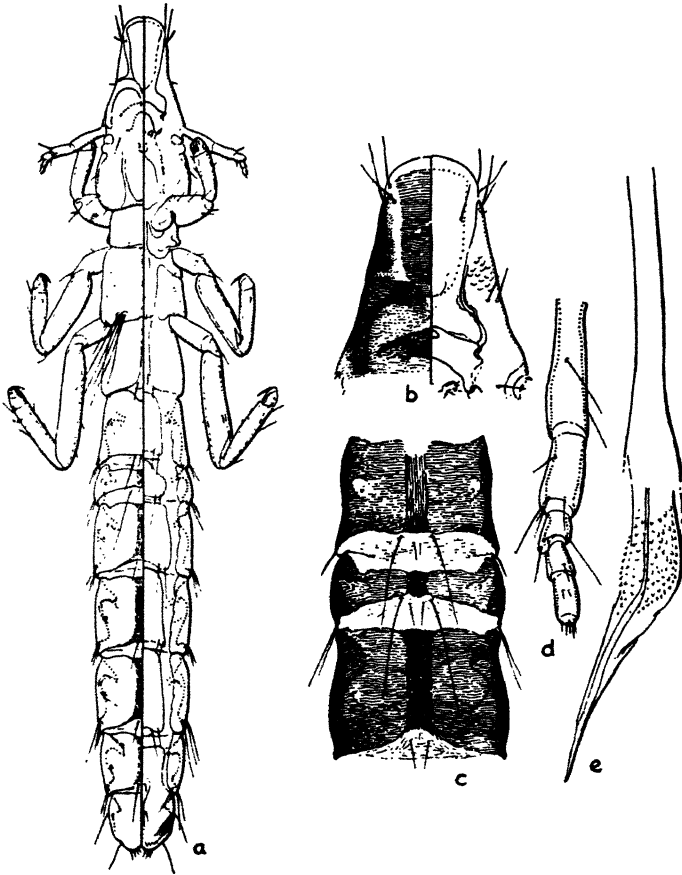


Figure 149—*Pectinopygus* (*Epifregata*) *gracilicornis* (Piaget): a, male; b, anterior part of head; c, flexing segment of abdomen; d, antenna of male; e, male genitalia. (After Ferris, 1932:61.)

Genus **PECTINOPYGUS** Mjoeberg, 1910

Thompson (1937:539) redefined this genus.

Pectinopygus (*Epifregata*) *gracilicornis* (Piaget) (fig. 149, a-e).

Lipeurus gracilicornis Piaget, 1880:309, pl. 25, fig. 6.

Esthiopterum gracilicornis (Piaget) Ferris, 1932:61, fig. 13, a-e.

Pectinopygus (*Epifregata*) *gracilicornis* (Piaget) Thompson, 1937:542.

Laysan, Necker.

Indigenous. First recorded from the leeward Hawaiian islands by Kellogg and Paine in 1910. Widespread.

Hosts: *Fregata minor palmerstoni* (aquila) (frigate bird), *Sterna lunata* (gray-backed tern).

Pectinopygus* (*Pectinopygus*) *sulae (Rudow) (fig. 150, a-b).

Lipeurus sulae Rudow, 1870:134.

Lipeurus gracilicornis variety *major* Kellogg, 1899:30, pl. 3, fig. 6.

Lipeurus potens Kellogg and Kuwana, 1902:477, pl. 30, fig. 1.

Pectinopygus (*Pectinopygus*) *sulae* (Rudow) Waterston, 1923:289. Ferris, 1932:64, figs. 16, a, b; 17, a-d.

See Thompson, 1939:211, for detailed synonymy.

Laysan, Necker.

Indigenous. First recorded from Laysan by Kellogg and Paine in 1910. Widespread.

Hosts: *Fregata minor palmerstoni* (aquila) (frigate bird), *Sterna lunata* (gray-backed tern), *Sula sula rubripes* (piscator) (red-footed booby).

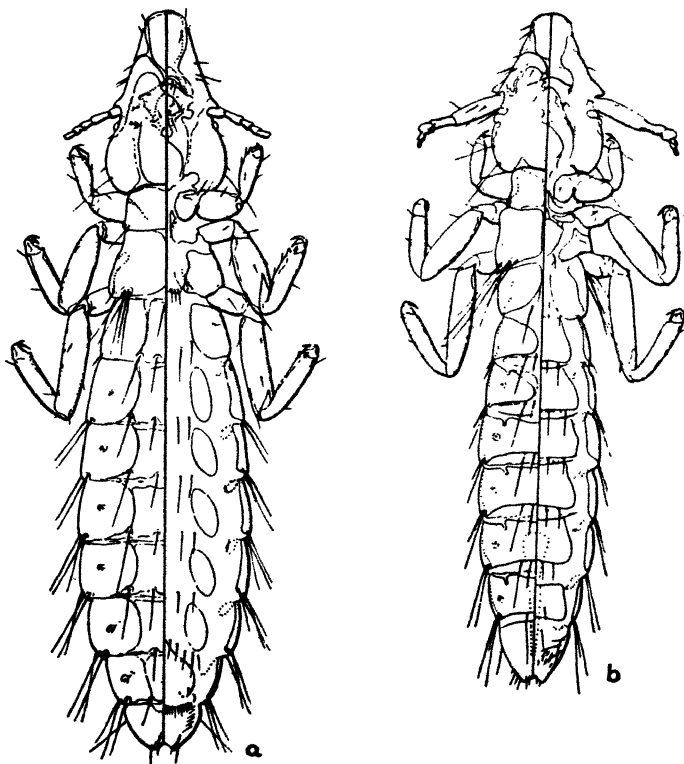


Figure 150—*Pectinopygus sulae* (Rudow): a, female; b, male. (After Ferris, 1932:65.)

Genus **HARRISONIELLA** Bedford, 1929**Harrisoniella ferox** (Giebel).

Lipeurus ferox Giebel, 1867:196.

Lipeurus densus Kellogg, 1896:114, pl. 7, figs. 1, 2.

Esthiopterum diomediae (Fabricius) Harrison, 1916:133.

Harrisoniella diomediae (Fabricius) Bedford, 1929:529.

Harrisoniella ferox (Giebel) Clay, 1940:298; see also pp. 299-302 for discussion of synonymy. Fabricius' species *diomediae* is a *Perineus* and distinct from this form.

Laysan.

Indigenous. Widespread. First recorded from the Territory by Kellogg and Paine in 1910.

Hosts: *Diomedea nigripes* (black-footed albatross), *Diomedea* (*Thalassarche*) *immutabilis* (Laysan albatross).

Cope (1940:117-142, figs. 54-66) gives a detailed account of the morphology of this species.

Genus **PERINEUS** Harrison, in Thompson, 1936:41**Perineus concinnus** (Kellogg and Chapman).

Lipeurus concinnus Kellogg and Chapman, 1899:97, pl. 7, fig. 2.

Perineus concinnus (Kellogg and Chapman) Harrison, 1937:29.

Laysan.

Indigenous. Described from California. First recorded from the Territory by Kellogg and Paine in 1910.

Host: *Diomedea* (*Thalassarche*) *immutabilis* (Laysan albatross).

Perineus giganticulum (Kellogg).

Nirmus giganticulum Kellogg, 1896:105, pl. 5, fig. 6.

Lipeurus confidens Kellogg, 1899:26, pl. 3, fig. 1.

Lipeurus miriceps Kellogg and Kuwana, 1902:480, pl. 30, fig. 4.

Perineus confidens (Kellogg) Thompson, 1936:42.

Laysan.

Indigenous. Widespread. First reported from the Territory in 1910 by Kellogg and Paine.

Hosts: *Diomedea nigripes* (black-footed albatross), *Sterna lunata* (gray-backed tern).

Genus **COLUMBICOLA** Ewing, 1929:116

Ewing separated this group of long, slender lice from *Esthiopterum* because the clypeus has on its dorsal surface two pairs of stout spines, one pair directed forward, the other pair directed upward and backward. The first antennal segment is enlarged in the male, is much larger than that of the female, and the third segment has its apex produced into a thumb-like process. The antennae of the female barely attain the hind margin of the head, whereas those of the male distinctly surpass it in length.

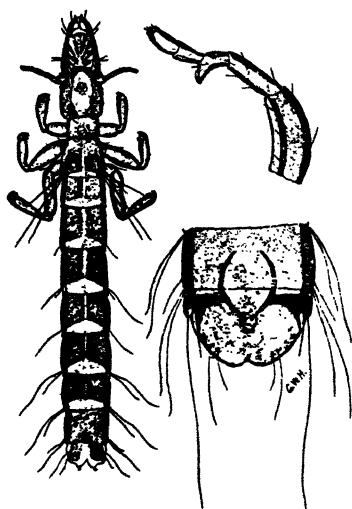


Figure 151—*Columbicola columbae* (Linnaeus), the pigeon louse: female, male antenna and apex of male abdomen. (After Herrick, 1915.)

Columbicola columbae (Linnaeus) (fig. 151).

Pediculus Columbae Linnaeus, 1758:614.

Lipeurus bacillus Nitzsch, 1874:215 (*baculus*, p. 216). pl. 16, figs. 8-9; pl. 20, fig. 3.

Columbicola columbae (Linnaeus) Ewing, 1929:117, fig. 66.

The pigeon louse.

Kauai, Oahu, Maui, Hawaii.

Immigrant. Widespread. First recorded in the Territory by me in 1944 from specimens collected in Honolulu in 1943.

Hosts: *Columba livia* (pigeon), *Geopelia striata striata* (barred-shoulder dove), *Streptopelia (Turtur) chinensis* (Chinese dove).

This is a common species on pigeons, and it may be found most abundantly on the flight feathers of the birds. Sodium fluoride dust will control it.

Martin (1934:6-16) has written an account of the biology of this louse. She found that the lice were dispersed, in part, by attaching themselves to the pigeon louse fly (*Pseudolynchia* [Hippoboscidae]). She reports that the lice feed almost exclusively on feather barbules, that the egg stage is about 4 days, and that the three nymphal instars have a duration of about 6.75 days. She gives illustrations of the eggs, three larval instars and the adult.

In 1938 I collected this species from a native fruit pigeon shot in the jungle of Viti Levu, Fiji.

Genus **LIPEURUS** Nitzsch, 1818

Lipeurus caponis (Linnaeus) (fig. 152. a-f).

Pediculus Caponis Linnaeus, 1758:614.

The variable chicken louse.

Kauai, Oahu, Hawaii and probably the other islands.

Immigrant. Cosmopolitan. First recorded from the Territory by Illingworth in 1928 from specimens found in Honolulu in 1926.

Hosts: chicken, *Phasianus colchicus torquatus* (Chinese pheasant).

Control: sodium fluoride dust gives good control.

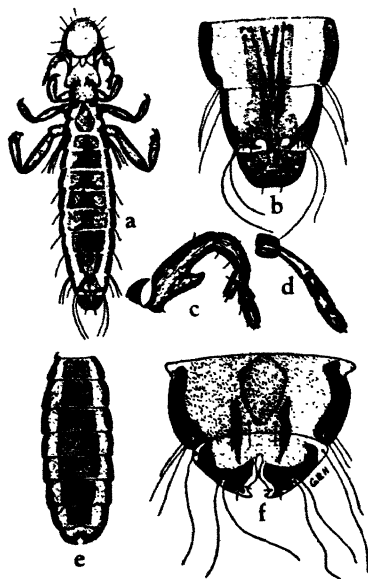


Figure 152—*Lipeurus caponis* (Linnaeus), the variable chicken louse: a, male; b, posterior end of female abdomen; c, male antenna; d, female antenna; e, female abdomen; f, two terminal abdominal segments of female. (After Herrick, 1915.)

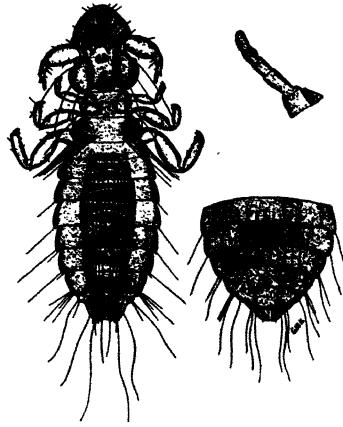


Figure 153—*Cuclostogaster heterographus* (Nitzsch): male, female antenna and end of female abdomen. (After Herrick, 1915.)

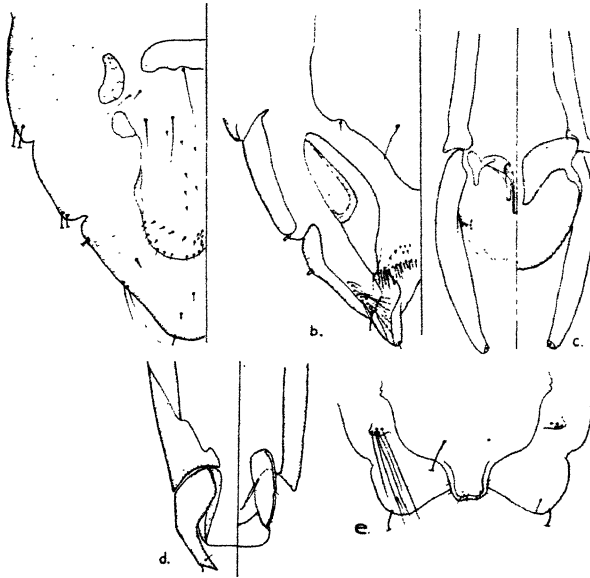


Figure 154—Details of the genitalia of some Mallophaga: a, *Cuclostogaster heterographus* (Nitzsch), posterior segments of female abdomen; b, the same of *Oxylipeurus polytrapezius* (Burmeister); c, genitalia of female of same species; d, *Lagopoecus docophoroides* (Piaget), male genitalia; e, *Oxylipeurus polytrapezius* (Burmeister), posterior abdominal segments of male. (Original drawings loaned by Miss Theresa Clay.)

Genus **CUCLOTOGASTER** Carriker, 1936

Gallipeurus Clay, 1938:135.

Cuclostogaster heterographus (Nitzsch) (figs. 153; 154, a).

Lipeurus heterographus Nitzsch, 1866:381.

Gallipeurus heterographus (Nitzsch) Clay, 1938:136, figs. 15, 16, 17, 18a.

Oahu and probably the other main islands.

Immigrant. Widespread. First recorded from the Territory in 1928 by Illingworth from specimens collected in Honolulu in 1926.

Host: chicken.

The usual control by the use of sodium fluoride is effective.

Genus **OXYLIPEURUS** Mjoeberg, 1910

Oxylipeurus polytrapezius (Burmeister) (figs. 154, b, c, e; 155).

Lipeurus polytrapezius Burmeister, 1838:434.

(*Pediculus galli-pavonis* Geoffroy, 1762:600, new edition, 1799:600, name used in our literature. The true *galli-pavonis* belongs to *Goniodes*: see Clay, 1938: 181, pl. 12, fig. 4, text figs. 37a, c, 39b, for explanation.)

The turkey louse.

Oahu and probably other islands.

Immigrant. Widespread. First recorded from the Territory by Illingworth in 1928 from specimens collected in Honolulu in 1926.

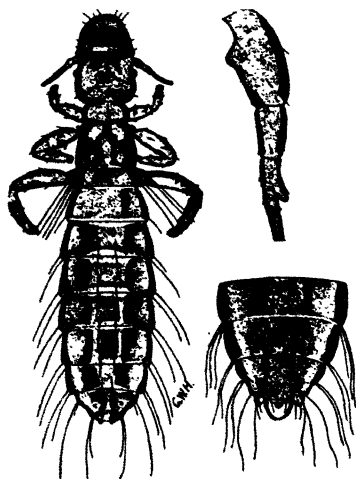


Figure 155—*Oxylipeurus polytrapezius* (Burmeister): female, male antenna and apex of male abdomen. (After Herrick, 1915.)

Host: turkey.

This species may become abundant on the flight feathers. Sodium fluoride dust is recommended for control.

Genus **LAGOPOECUS** Waterston, 1922

Lagopoecus docophoroides (Piaget) (fig. 154, d).

Lipeurus docophoroides Piaget, 1880:351, pl. 28, fig. 9.

Lipeurus docophoroides variety *minhaensis* Kellogg and Chapman, 1902:159; 1904:310. Described from Lahaina, Maui. First record for Hawaii.

Lipeurus minhaensis (Kellogg and Chapman) Thompson, 1939:16. Synonymy by Clay, 1938:195, fig. 43d.

Maui.

Immigrant. Described from California.

Host: Kellogg and Chapman gave the host as *Acridotheres tristis*, the mynah, but this must have been recorded from a straggler. The true host is evidently the quail. It was described from the California quail, *Lophortyx californica californica*. I have no further notes on this species.

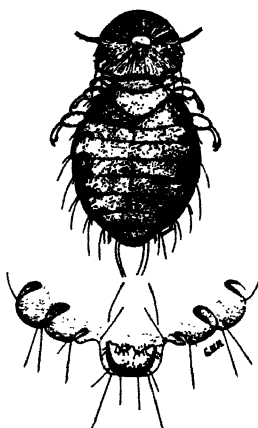


Figure 156—*Goniocotes hologaster* (Nitzsch), the fluff louse; male, above; enlarged sketch of apex of female abdomen, below. (After Herrick, 1915.)

Genus **GONIOCOTES** Burmeister, 1838

The members of this genus, together with those of *Goniodes*, have a characteristic, broad appearance. Most of the species are found on gallinaceous and columbine birds.

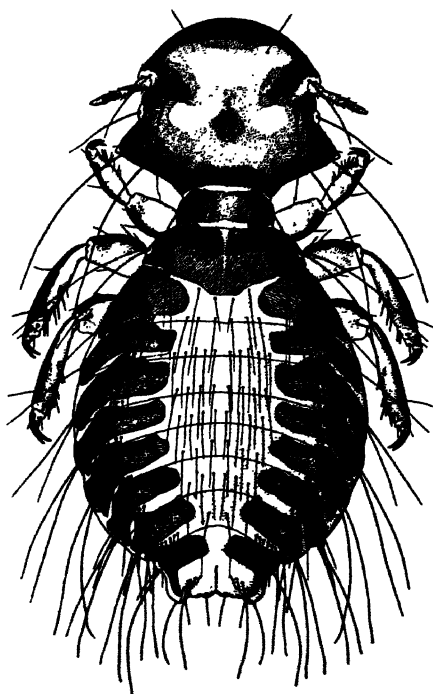


Figure 157—*Goniodes dissimilis* Denny, female. (After Clay, 1940; drawing by Terzi.)

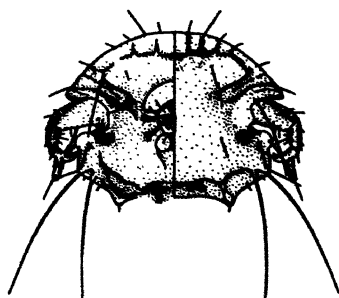


Figure 158—*Goniodes dissimilis* Denny, head of male. (After Clay, 1940.)

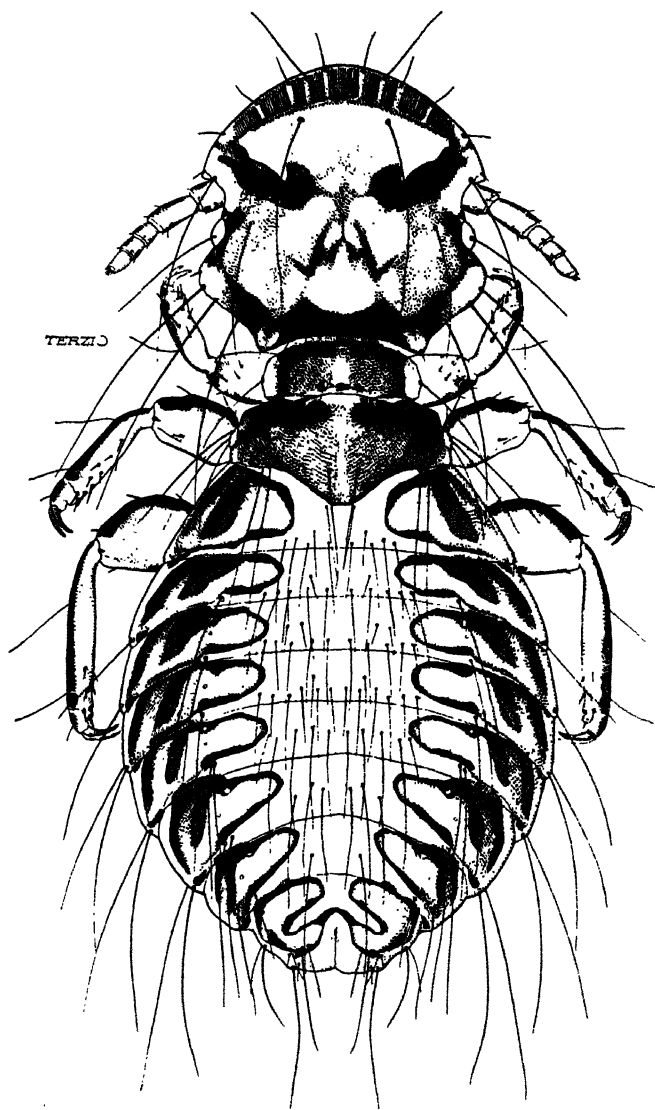


Figure 159—*Goniodes gigas* (Taschenberg), the large chicken louse, female. (After Clay, 1940.)

Goniocotes chinensis Kellogg and Chapman (fig. 145, f).

Goniocotes chinensis Kellogg and Chapman, 1902:160, pl. 13, fig. 5; 1904:311, pl. 10, fig. 5.

Kauai, Maui (type locality: Kahului), Hawaii.

Immigrant, but not recorded elsewhere.

Hosts: *Streptopelia* (*Turtur*) *chinensis* (Chinese dove), *Geopelia striata striata* (barred-shoulder dove).

Goniocotes hologaster Nitzsch (fig. 156).

Goniocotes hologaster Nitzsch, 1838:431.

The fluff louse.

Oahu, Hawaii and probably on the other islands.

Immigrant. First recorded from the Territory by Illingworth in 1928 from specimens collected in Honolulu in 1926.

Hosts: chicken, turkey, *Phasianus colchicus torquatus* (Chinese pheasant).

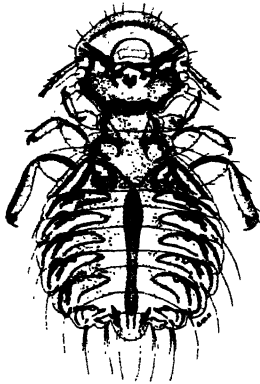


Figure 160—*Goniodes gigas* (Taschenberg) male. (After Herrick, 1915.)

Genus **GONIODES** Nitzsch, 1818

The members of this genus, like those of *Goniocotes*, are partial to gallinaceous birds.

In addition to the following four species, *Goniodes paxonis* (Linnaeus), on peafowl, may also be found in Hawaii, but it has not yet been recorded here.

Goniodes dissimilis Denny (figs. 157, 158).

Goniodes dissimilis Nitzsch, 1818:294.

Goniodes dissimilis Denny, 1842:57, 162, pl. 12, fig. 6. Clay, 1940:62, figs. 41–43.

Oahu.

Immigrant. Widespread. Not recorded from the Territory heretofore, but I have specimens before me which were taken from a chicken in Nuuanu Valley in 1932 and kindly identified for me by Mr. G. B. Thompson.

The illustrations serve to distinguish this species easily from *G. gigas*, the other *Goniodes* occurring on chickens in Hawaii. The third antennal segment of the male of this species has a prominent process, whereas that of *gigas* has no process.

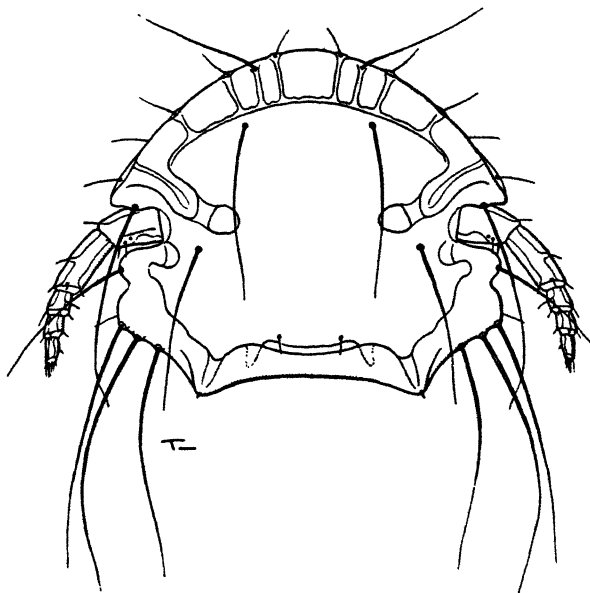


Figure 161—*Goniodes gigas* (Taschenberg), head of male. (After Clay, 1940.)

Goniodes gigas (Taschenberg) (figs. 159, 160, 161).

Goniocotes gigas Taschenberg, 1879:104, pl. 1.

Goniodes gigas (Taschenberg) Clay, 1940:33, figs. 21–22.

The large chicken louse.

Kauai, Oahu, and probably on the other main islands.

Immigrant. Widespread. First recorded from Hawaii by Illingworth in 1928 from specimens collected at Waipio, Oahu, in 1926.

Hosts: guinea fowl, domestic chicken. Thompson (1938:188) and Clay (1940:33) say that the guinea fowl is the normal host.

Goniodes lativentris Uchida.

Goniodes lativentris Uchida, 1916:81, figs. 1, 2.

Oahu.

Immigrant. Described from Japan. First found in Hawaii in 1945 by a member of the armed forces, but not recorded in Hawaiian literature heretofore.

Host: "dove." (The dove the Hawaiian specimens were obtained from was either *Streptopelia chinensis* or *Geopelia striata*; I do not know which).

Goniodes mammillatus Rudow (fig. 162, a-c).

Goniodes mammillatus Rudow, 1870:483. Clay, 1940:60, fig. 40.

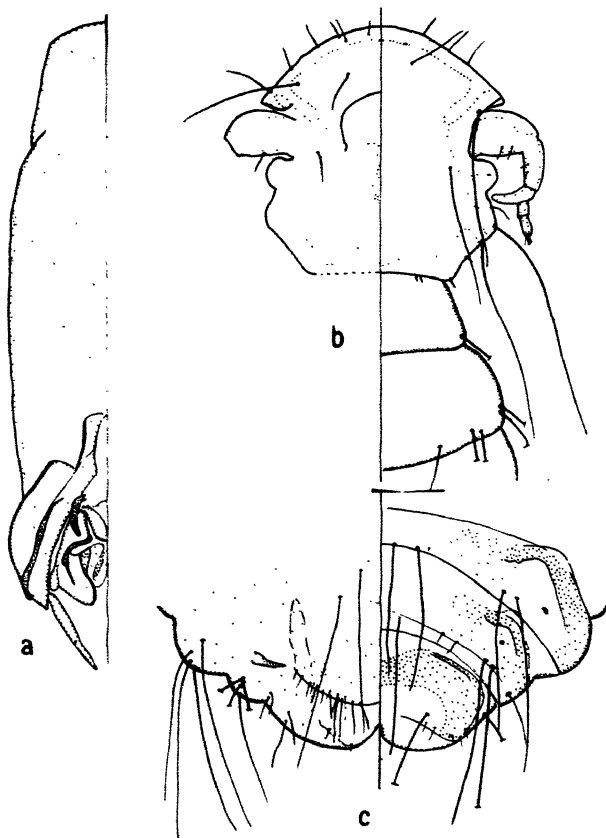


Figure 162—*Goniodes mammillatus* Rudow; a, male genitalia; b, head and thorax; c, apex of female abdomen. (Original drawings loaned by Miss Theresa Clay.)

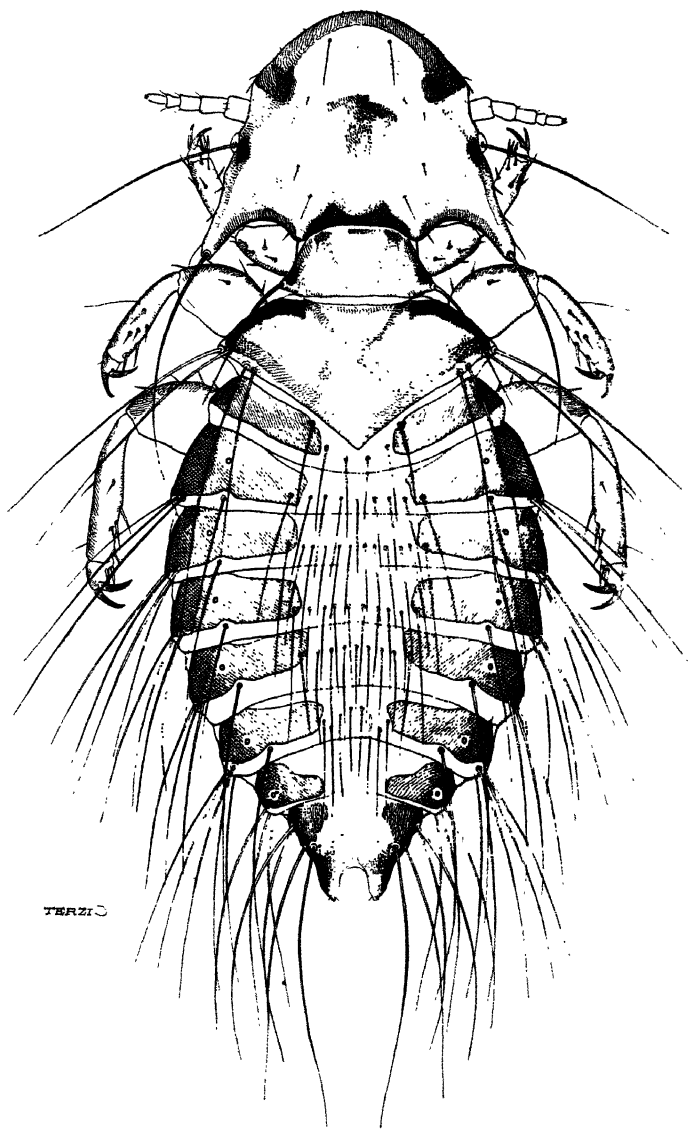


Figure 163—*Chelopistes meleagridis* (Linnaeus), the large turkey louse, female. (After Clay, 1941; cut loaned by Parasitology.)

Hawaii.

Immigrant. Widespread. First recorded from the Territory by me in 1943 (1944:200) from specimens collected by Paul Baldwin in Hawaii National Park in 1938. Described from Europe.

Host: *Lophortyx californica vallicola* (California valley quail). Essig (1929) records it from grouse and ptarmigans in western North America. I have seen an example from a pheasant from Hawaii.

Genus **CHELOPISTES** Kéler, 1939:180

Virgula Clay, 1941:119.

Chelopistes meleagridis (Linnaeus) (figs. 163; 164; 165, a-b; 166, a-c).

Pediculus Meleagridis Linnaeus, 1758:613.

Goniodes stylifer Nitzsch, 1838:432. Genotype of *Chelopistes*.

Virgula meleagridis (Linnaeus) Clay, 1941:119, figs. 1-4.

The large turkey louse.

Oahu, Molokai.

Immigrant. Widespread; described from Europe. First recorded from the Territory by Van Dine in 1909 from material collected on Molokai.

Hosts: turkey, chicken.

This common louse of turkeys will yield to control by sodium fluoride dust.

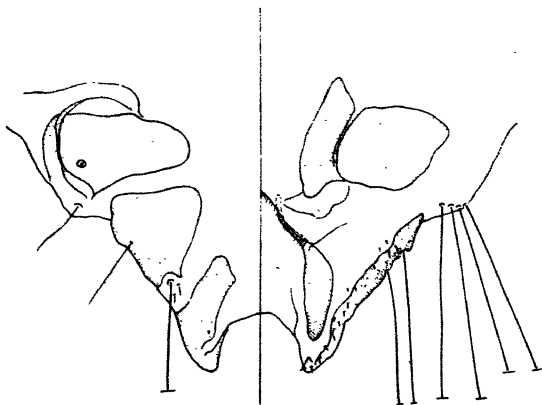


Figure 164—*Chelopistes meleagridis* (Linnaeus), terminal abdominal segments of female. (After Clay, 1941; cut loaned by *Parasitology*.)

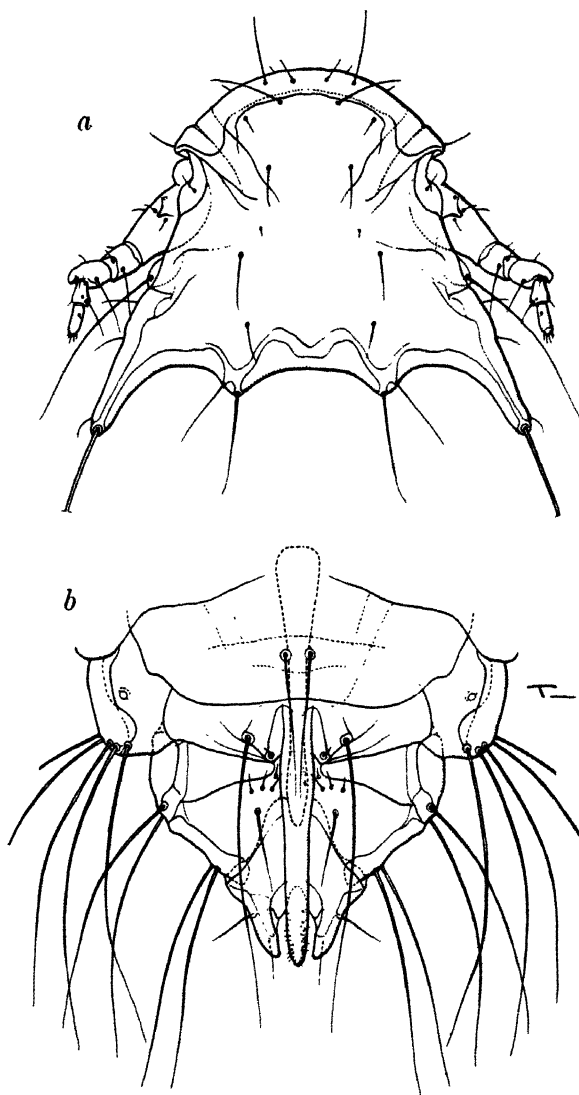


Figure 165—*Chelopistes meleagridis* (Linnaeus), male: a, head; b, terminal abdominal segments. (After Clay, 1941; cut loaned by *Parasitology*.)

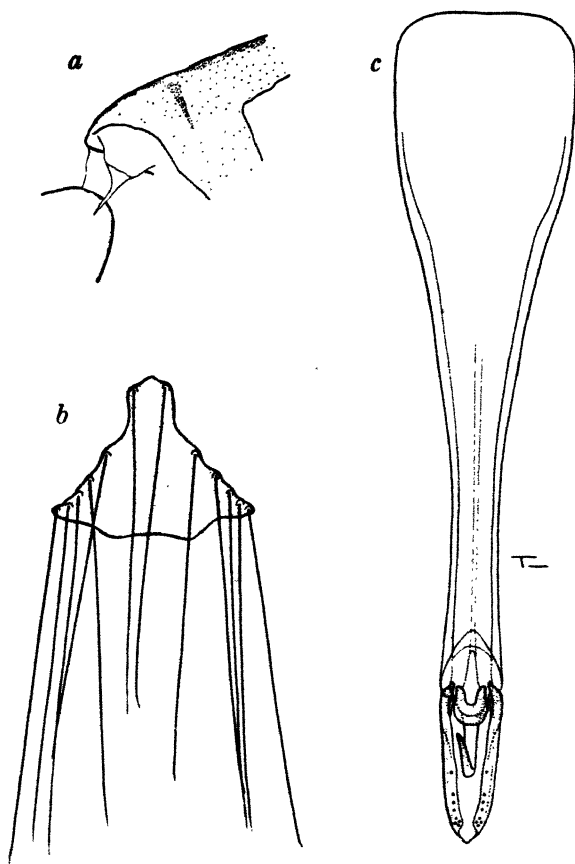


Figure 166—*Chelopistes melcagridis* (Linnaeus), details of male: **a**, clavi; **b**, sternal thoracic plate; **c**, genitalia. (After Clay, 1941; cut loaned by *Parasitology*.)

SPECIES INCERTAE SEDIS

The following two species appear not to belong to the genera to which they have been assigned. The types must be examined before they can be placed in systematic order.

Degeeriella (?) diaprepes (Kellogg and Chapman) (fig. 167).

Nirmus diaprepes Kellogg and Chapman, 1902:158, pl. 13, fig. 4; 1904:309, pl. 10, fig. 4.

Degeeriella diaprepes (Kellogg and Chapman) Thompson, 1939:75.

Endemic(?). Hawaii (type locality: Hilo).

Host: *Vestiaria coccinea* ("iwi").

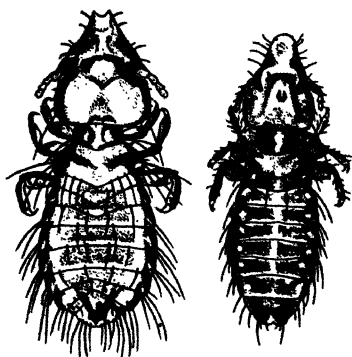


Figure 167—*Degeeriella* (?) *diaprepes* (Kellogg and Chapman), male, left; *Degeeriella* (?) *minhaensis* (Kellogg and Chapman), female, right. (Rearranged from Kellogg and Chapman, 1904.)

Degeeriella (?) *minhaensis* (Kellogg and Chapman) (fig. 167).

Nirmus minhaensis Kellogg and Chapman, 1902:157, pl. 13, fig. 2; 1904:307, pl. 10, fig. 2.

Degeeriella minhaensis (Kellogg and Chapman) Thompson, 1939:120.

Maui (type locality: Lahaina).

Immigrant; status uncertain.

Host: *Acridotheres tristis* (mynah).

While this volume was in proof, "Mallophaga Collected by the Tanager Expedition" by G. B. Thompson (1948) has come to hand. It includes several species new to Hawaii, as follows:

Austromenopon (?) *infrequens* (Kellogg, 1896), Pearl and Hermes Reef, on *Laurus hyperboreus*. *Austromenopon sternophilum* (Ferris, 1932), Laysan, on *Anous stolidus pilcatus*. *Actornithophilus milleri* (Kellogg and Kuwana, 1902), Laysan, on *Anous stolidus pilcatus*. *Longimenopon puffinus* Thompson (a new genus and species), Laysan, on *Puffinus pacificus cuneatus* and *Puffinus nativitatis*. *Saemundssonina* (?) *gonothorax* (Giebel, 1871), Pearl and Hermes Reef, on *Laurus hyperboreus*. *Lunaceps* species (?), Laysan, on *Numenius tahitiensis*. *Halipeurus mirabilis* Thompson, 1940, Laysan, on *Puffinus pacificus cuneatus* and *Diomedea nigripes*. *Harrisoniella* species (?), Laysan and Ocean Islands, on *Diomedea immutabilis* and *Diomedea nigripes*. *Giebelia* (?) *mirabilis* Kellogg, 1896, Laysan, on *Puffinus pacificus cuneatus*. *Docophoroides* species (?), Laysan, on *Diomedea immutabilis*.

The bibliography for this section is combined with that of the Anoplura and appears at the end of the section on Anoplura (p. 315).

Order ANOPLURA Leach, 1815

(*anoplus*, unarmed; *oura*, tail)

Sucking Lice

Aptera Linnaeus, 1758, in part.

Parasita Latreille, 1802, in part.

Anoplura Leach, 1815.

Siphunculata Latreille, 1825.

Pediculina Burmeister, 1835.

Pediculida Mayer, 1876.

Polyptera Banks, 1892.

Pediculoidea Crampton, 1921.

Hemiptera, suborder *Parasita*, Comstock and Comstock, 1895.

Hemiptera, suborder *Parasitica*, Osborn, 1923.

Psocoida Weber, 1939, in part.

According to the law of priority, the correct name for this order appears to be *Parasita* Latreille, as has been recently pointed out by Essig (1942:202). However, the term *Anoplura* has been in use for so long that perhaps more confusion than uniformity would result from the usage of *Parasita* in place of *Anoplura*. The term *Anoplura* should probably be stabilized through the provision made by the International Rules for Zoological Nomenclature for *nomina conservanda*.

Body elongate, depressed, soft, but integument tough. Head prognathous, exposed mouth parts retractile, highly modified for piercing skin and sucking blood, haustellum present, mandibles obsolete, palpi absent, maxillae and labium greatly modified into dorsal and ventral piercing stylets, labrum inverted as the roof of the fore part of the buccal cavity, hypopharynx tube-like, enclosing the salivary duct; antennae short, exposed, filiform, three- to five-segmented; eyes present or absent, reduced if present; ocelli absent. Thorax usually small, segmentation obscure or obsolete, with one or more pairs of dorsal spiracles. Wings or wing rudiments absent. Legs strongly modified for grasping hair of hosts, with single-segmented tarsi bearing single claws. Abdomen apparently nine-segmented; cerci absent; spiracles on segments three to eight or two to eight; male genitalia well developed, comparatively simple; female genitalia without an ovipositor, but with a pair of gonopods used in placing the eggs on hairs at oviposition. Eggs (called nits) normally cemented singly to hairs of host; metamorphosis absent; four instars. Bloodsucking, permanent, obligatory, ectoparasites of mammals exclusively. Size range from 0.25 mm. in a species from American flying squirrels to over 6 mm. in a species from an African wart hog.

There are nearly 250 species of sucking lice known today. No fossil forms have been found. The order is world-wide in distribution, and the host relationships are most interesting. The lice of man and primates are allied, and no louse of man is related to any louse not found on primates. The majority of species are found on rodents, hoofed animals and primates. The only carnivores harboring sucking lice are dogs (one louse species) and such marine mammals as seals, sea lions, walruses, etc. The cat family is free from sucking lice and the marsupials, bats, edentates and insectivores (with only a few exceptions) are likewise not attacked by these lice. As a continent, Australia is remarkably free from sucking lice; however, there are native Anoplura on the endemic rodentia and marine mammals. Perhaps Australia was isolated by sea from Asia before this group of lice became extensively developed and widespread. No insect parasites of the order are known. All eight of the sucking lice found in Hawaii are immigrants. Only three forms attack man.

Various members of the order play an important role in the dissemination of the causative organisms of a number of serious diseases, some of which will be discussed in appropriate places below.

TABULAR ANALYSIS OF THE HAWAIIAN ANOPLURA

FAMILY	GENERA	ENDEMIC GENERA	NON- ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Haematopinidae	4	0	4	6	0	6
Pediculidae	2	0	2	2	0	2
Totals	6	0	6	8	0	8

Fauna 100 percent adventive.

Average number of species per genus: 1.3.

KEY TO THE FAMILIES OF ANOPLURA FOUND IN HAWAII

1. Eyes absent; on domesticated animals and rodents in Hawaii
..... **Haematopinidae.**
2. Eyes present; on man in Hawaii..... **Pediculidae.**

In addition to these two families, it is probable that members of the Echinophthiridae would be found, if searched for, on the seals which occasionally are seen in the leeward Hawaiian Islands. No lice have been reported from various imported mammals in the islands, and a detailed survey would probably reveal several immigrant species not listed in this chapter.

Family HAEMATOPINIDAE Enderlein, 1904

The members of this family are principally characterized by having the body setae arranged in rows, squamae absent, head not tubularly produced in front, tibiae without a thumb-like process and eyes absent. They are principally found on hoofed animals and rodents.

In addition to the species recorded here, it is probable that the sucking rabbit louse, *Haemodipsus ventricosus* (Denny), is also present in the islands.

KEY TO THE SUBFAMILIES OF HAEMATOPINIDAE FOUND IN HAWAII

1. All pairs of legs more or less similar; each tarsus and tibia fitted for clasping hairs. **Haematopininae.**
Anterior legs smaller than other two pairs; not all of tarsi and tibiae fitted for clasping hairs. 2
2. Pleural plates distinct on at least some abdominal segments **Hoplopleurinae.**
Pleural plates of abdominal segments wanting or obsolete. **Linognathinae.**

Subfamily HAEMATOPININAE Enderlein, 1904

Genus HAEMATOPINUS Leach, 1815

The species of this genus are found only on the ungulate families Suidae, Camelidae, Bovidae, Cervidae and Equidae. The largest species of sucking lice belong to this genus. For a monograph of the genus with extensive discussion, see Ferris, 1933:1-56.

These lice may be controlled by the use of 10 percent DDT dust, sodium fluoride and similar dusts; a number of standard dips, emulsions and greases (including crankcase oil) are recommended by various workers.

KEY TO THE SPECIES OF HAEMATOPINUS FOUND IN HAWAII

1. Head comparatively short and broad, only slightly longer than broad; on cattle. **eurysternus** (Nitzsch).
Head two to three times as long as broad; not on cattle. 2
2. On horses: head unusually long, one-half as long as remainder of body. **asini** (Linnaeus).
On swine: head less than half as long as remainder of body. **suis** (Linnaeus).

Haematopinus asini (Linnaeus) (fig. 168).

Pediculus Asini Linnaeus, 1758:612.

See Ferris, 1933:50, for synonymy and detailed discussion.

The sucking horse louse.

Oahu, Hawaii (and the other islands ?).

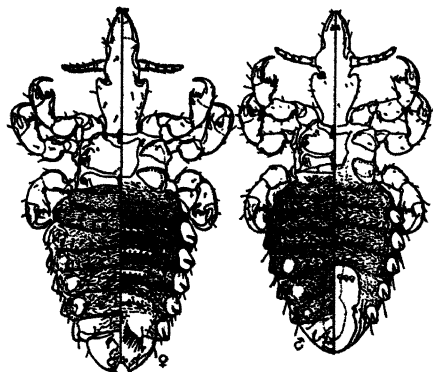


Figure 168—*Haematopinus asini* (Linnaeus), the sucking horse louse. (After Ferris, 1933.)

Immigrant. Nearly cosmopolitan. This species has not been recorded from the Territory heretofore, but I have seen specimens collected at Naalehu, Hawaii, in 1905 and have had a report of a recent infestation at Schofield Barracks on Oahu.

***Haematopinus eurysternus* (Nitzsch) (fig. 169).**

Pediculus eurysternus Nitzsch, 1818:305 (I have not checked this reference).

See Ferris, 1933:34, for synonymy, description, discussion and detailed illustrations.

The short-nosed ox louse.

Oahu, Hawaii (and the other islands?).

Immigrant. Nearly cosmopolitan. First recorded from the Territory by Ferris in 1933 from specimens collected from a dog (an abnormal host record) in Honolulu by the late E. M. Ehrhorn.

Host: normally cattle.

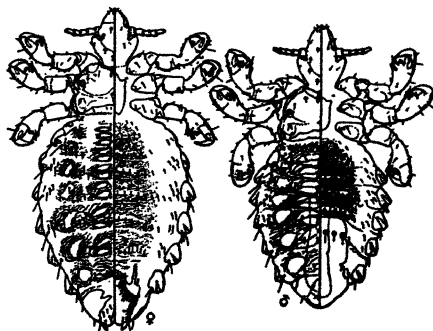


Figure 169—*Haematopinus eurysternus* (Nitzsch), the short-nosed ox louse. (After Ferris, 1933.)

Little is known of this louse in Hawaii, and it is apparently uncommon. Only one of 376 Hawaiian cattle examined by A. C. Cuckler in 1941 (1943:48) was found infested. Perhaps the best place to search for these lice on animals is along the inner edges of the ears.

***Haematopinus suis* (Linnaeus) (fig. 170).**

Pediculus Suis Linnaeus, 1758:611.

See Ferris, 1933:11-30, for detailed synonymy, discussion and figures; Florence, 1921:637-743, for biology, anatomy, histology.

The hog louse; Hawaiian name: "uku pua'a."

Oahu, Lanai. Surely on all of the Hawaiian Islands wherever swine are found, but not definitely recorded in literature.

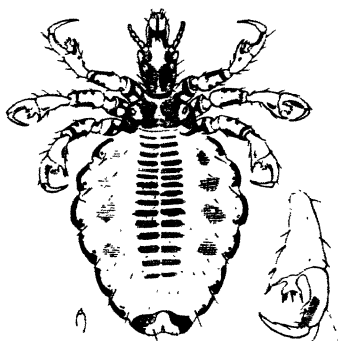


Figure 170—*Haematopinus suis* (Linnaeus), the hog louse, female. (Abernathy drawing.)

Immigrant. Cosmopolitan. The earliest Hawaiian record printed in entomological literature which I have seen is that by Illingworth in 1928 (p. 43). However, this louse was well known to the old Hawaiians, for it was brought in by them when they introduced their pigs from the South Seas during their early voyages in canoes. It is unfortunate that we do not have specimens of some of the lice originally found on the "Hawaiian" pig. Its race or variety might have supplied some interesting information.

Host: swine.

The hog louse is a vector of swine pox, and whenever that disease breaks out control measures against the louse should be undertaken immediately. Heavy infestations are not recorded frequently in Hawaii.

Subfamily HOPLOPLEURINAE

The species of this family found in Hawaii are confined to rats and mice.

KEY TO THE GENERA OF HOPLOPLEURINAE FOUND IN HAWAII

1. With at most two transverse rows of setae on most of abdominal tergites in female, but only a single row in male; third segment of antenna of male with a process and unlike that of female **Polyplax** Enderlein.
2. With three rows of setae on most of abdominal tergites in female, and two rows in male; antennae similar in both sexes and not modified in male..... **Hoplopleura** Enderlein.

Genus **POLYPLAX** Enderlein, 1904:142

The species of this genus are almost entirely confined to rats and mice. A single species has been found in Hawaii. See Ferris (1923:183-237) for monographic details.

Polyplax spinulosa (Burmeister) (fig. 171).

Pediculus spinulosus Burmeister, 1838:8.

Polyplax spinulosa (Burmeister) Enderlein, 1904:142. Genotype.

For detailed synonymy and discussion, see Ferris, 1923:187, and figs. 119, 120A,D,F,H.

The spinulose rat louse.

Oahu and probably on the other islands.

Immigrant. Cosmopolitan. This species was first reported by me in 1943 (1944: 200) from specimens taken earlier in Honolulu.

Hosts: According to Ferris, it is a normal parasite of *Rattus rattus* and *Rattus norvegicus* wherever they occur and is also found on other rats and mice.

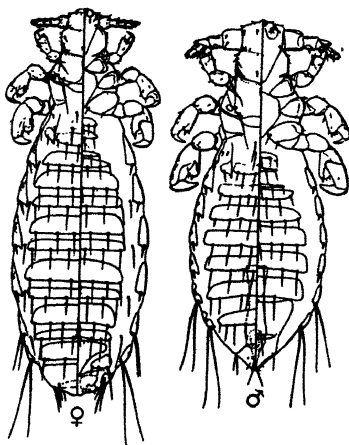


Figure 171—*Polyplax spinulosa* (Burmeister). (After Ferris, 1923.)

This louse transmits *Trypanosoma lewisi* (apparently non-pathogenic) from rat to rat, and it is a normal carrier of murine or endemic typhus fever from rat to rat.

Genus **HOPLOPLEURA** Enderlein, 1904:221.

Although some species are found on other groups of mammals, the members of this genus are more characteristic of the rats, mice and squirrels (Muridae and Sciuridae). For detailed description and discussion of the genus, see Ferris, 1921:59–133. It is the largest genus of sucking lice.

Hoplopleura oenomydis Ferris (figs. 172; 173, a–e).

Hoplopleura oenomydis Ferris, 1921:82, figs. 47, 48.

Hoplopleura pacifica Ewing, 1924:9, figs. 1, b–c. Type locality: "Hawaiian Islands." Synonymy by Ferris, 1932:121, figs. 37, a–i; 38, a–k; 39, a–e.

The Pacific rat louse.

Oahu. Probably on the other islands, but no definite locality data assembled or available. First listed from Hawaii by Ewing (1924).

Immigrant. Also recorded from East Africa, the Philippines, Malaya, Sumatra, Celebes, Australia, Samoa, and the Marquesas Islands.

Hosts: several species of rats, including the Hawaiian rat.

Although Ewing (1924) stated that the type slide of his *H. pacifica* from the Hawaiian Islands had been placed in the Bishop Museum, the type material does not appear to be in the type collection.

See Ferris, 1932:121–127, for an extensive discussion of this species.

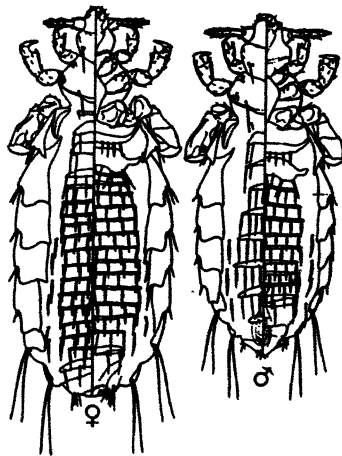


Figure 172—*Hoplopleura oenomydis* Ferris. (After Ferris, 1921.)

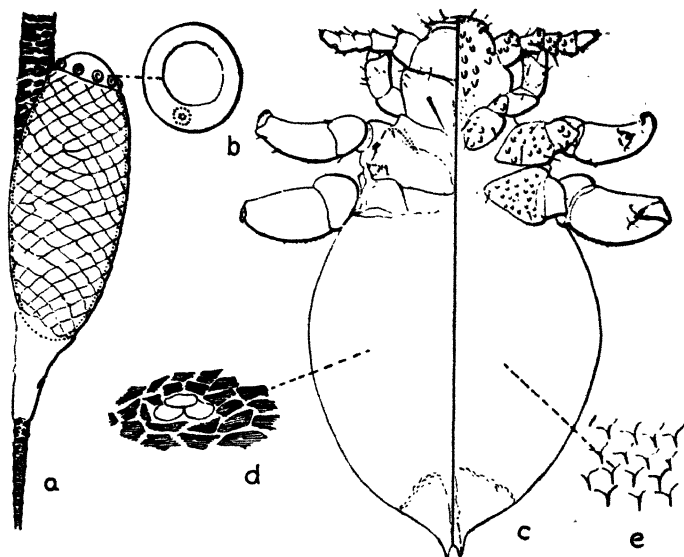


Figure 173—*Hoplopleura oenomydis* Ferris: a, egg; b, detail of egg; c, last stage of nymph; d, ornamentation of derm of dorsum; e, ornamentation of derm of venter. (After Ferris, 1932:126.)

Subfamily **LINOGNATHINAE**

Genus **LINOGNATHUS** Enderlein, 1905

"With the exception of a single species, which occurs on members of the family Canidae of the Order Carnivora, all the known species are from hosts of the ungulate Order Artiodactyla. Within this Order the hosts, with the single exception of one species of the family Giraffidae, are members of the family Bovidae, the cattle, sheep, goats, antelopes and similar forms. The genus may, in fact, be regarded as characteristic of this family." (Ferris, 1932:67.)

This genus can be distinguished from the other Anoplura found in Hawaii by the following combination of characters: eyes absent; antennae five-segmented, not sexually dimorphic; spiracles on abdominal segments three to eight inclusive; abdominal tergal and sternal plates absent, except for the caudal ones.

In addition to the two species below, some or all of the following *Linognathus* species may be established or may become established in Hawaii: *L. pedalis* (Osborn) on sheep, *L. stenopsis* (Burmeister) on goats, *L. vituli* (Linnaeus) on cattle.

Linognathus africanus Kellogg and Paine (fig. 174).

Linognathus africanus Kellogg and Paine, 1911:146. pl. 4, figs. 1, 5.

For synonymy, description and figures, see Ferris, 1932:83.

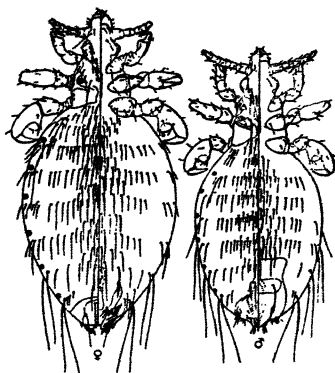


Figure 174—*Linognathus africanus* Kellogg and Paine. (After Ferris, 1932.)

The sucking goat louse.

Oahu, and probably on the other islands.

Immigrant. First collected in Hawaii by me when I found it abundant on goats at Kahala, Honolulu, in 1943. It was first described from sheep from southern Algeria, and it is now recorded from sheep and/or goats from Africa, North America, India and the Philippines; also recorded from "Klip Springer" in Africa.

Host in Hawaii: goat.

Ferris (1932:83) says, "On the basis of present knowledge it appears probable that some of the records of *L. stenopsis* from goats refer at least in part to this species." I found only specimens of this species and no *L. stenopsis* on the herd of goats from which I collected my first Hawaiian specimens, but a more detailed search might have revealed both species.

This louse was abundant and was causing considerable annoyance to goats—especially the kids, on which it was most common—when I first saw it in Honolulu.

Control: arsenical or nicotine dips or raw linseed oil worked into the infested areas is recommended; sodium fluoride and the new DDT dusts should be tried.

***Linognathus setosus* (Olfers) (fig. 175).**

Pediculus setosus Olfers, 1816, in "De vegetativis et animatis corporibus in corporibus animatis reperiundis commentarius," which I have not seen.

Pediculus piliferus Burmeister, 1838:13.

Genotype of *Linognathus*.

For detailed synonymy, discussion and illustrations, see Ferris, 1932:70.

The sucking dog louse.

Oahu (and the other islands?).

Immigrant. Cosmopolitan. Not recorded in Hawaiian literature heretofore.

Host: dog.

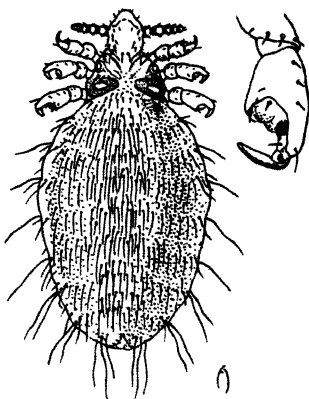


Figure 175—*Linognathus setosus* (Olfers). (Abernathy drawing.)

Family PEDICULIDAE Samouelle, 1819

The members of this family share the characters of the Haematopinidae in having the body setae arranged in definite rows, scales wanting, head not tubularly produced in front, tibiae without a thumb-like process, but the eyes are present and well pigmented.

It is evolutionarily significant that the Pediculidae are restricted to men, monkeys and apes. No species of the family lives on any but a primate host.

KEY TO THE SUBFAMILIES OF PEDICULIDAE

1. Fore legs fully as stout as other two pairs; abdomen distinctly segmented, lateral tubercles absent; thorax narrower than abdomen (fig. 176) **Pediculinae.**
2. Fore legs distinctly more slender than other pairs; abdomen not distinctly segmented, segments five to eight with conspicuous lateral tubercles; thorax broader than abdomen (fig. 177) **Phthirinae.**

Subfamily PEDICULINAE Enderlein, 1904

Although none has been yet recorded from Hawaii, it is possible that one or more species of *Pedicinus* are present on monkeys in the local animal park. To my knowledge, these animals have not been searched for lice.

Genus **PEDICULUS** Linnaeus, 1758:610

For a scholarly dissertation on the genus, replete with excellent illustrations, see Ferris, 1935:8-76, figs. 306-334, pls. 1-3.

The genus *Pediculus* is taxonomically difficult and confusing. The animals are variable, and a number of "species" and "varieties" have been described. After

long and careful study, Ferris (1935) concludes that there are but three recognizable, described, full species. One of these is the normal ectoparasite of man, another is found on New World monkeys, and the third is from a chimpanzee.

***Pediculus humanus humanus* Linnaeus.**

Pediculus humanus Linnaeus, 1758:610.

This form has also been called *corporis* and *vestimenti* by various authors.

The body louse, gray back, cootie; Hawaiian name: " 'uku kapa." "Kapa" is the Hawaiian spelling of "tapa," or bark cloth, which was used for clothing and bedding by the old Hawaiians.

***Pediculus humanus capitis* Degeer (fig. 176).**

Pediculus humanus variety *capitis* Degeer, 1778:67.

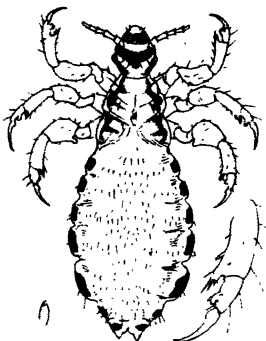


Figure 176—*Pediculus humanus capitis* Degeer, the human head louse, female. (Abernathy drawing.)

The head louse; Hawaiian name: " 'uku-po'o"; egg (nit), "liha."

For a detailed, scholarly discussion, complete synonymy and abundant illustrations, see Ferris, 1935:17-62, figs. 306-327, pls. 1-3. For anatomy, biology, medical importance and control, the excellent volume *The Louse* by Buxton, 1939, is highly recommended and it will give a key to literature for those who wish more detailed information than that included herein.

Immigrant. Cosmopolitan. Brought to Hawaii with the first aboriginal immigrants.

The human louse has been associated with man since the "beginning," and it is found with every race of man throughout the world, no matter what remote area he has colonized. Occasionally, specimens are found on primates in captivity and occasionally are taken from domesticated animals, but these are abnormal and unsuitable hosts.

Perhaps the earliest reference to human lice in Hawaiian literature is that made

by the missionary C. S. Stewart in 1828 (*Journal of a Residence in the Sandwich Islands, during the Years 1823, 1824 and 1825*. London, 1828). Stewart wrote that dozens of head lice

may, at any time, be seen sporting among the decorated locks of ignoble heads; while not infrequently, a privileged few wend their way through the garlands of princes of the blood, or triumphantly mount the coronets of majesty itself.

As to the servants of the chief and the common people, we think ourselves fortunate indeed, if, after a call of a few minutes, we do not find living testimonies of their visit, on our mats and floors, and even on our clothes and persons! The bare relation of the fact, without the experience of it, is sufficiently shocking. But the half is not told; and, I scarce dare let the truth, here, run to its climax. The lower classes not only suffer their heads and tapas to harbour these vermin; but they openly and unblushingly *eat them!* Yet so fastidious are they in point of cleanliness, that an emetic could scarce be more efficaciously administered than to cause them to eat from a dish in which a fly had been drowned!

Inasmuch as the old Hawaiians had lice, it is natural to expect that they would have stories about them. There are a number of Hawaiian place names that refer to lice, for example, Wainaukepo'o in Kau, Hawaii, refers to a place where it used to be the custom to rest by a stream side for purposes of delousing the head. A Hawaiian riddle runs:

"Ku'u kanaka holoholo iloko o ke 'uki," or, My man who runs around among the "uki" grass. Answer: a head louse.

The act of delousing is called "nauke" in Hawaiian. If the lice are killed by crushing between the fingernails, the process is called "ho'u'ina" (to snap), but if they are killed by biting, as is done by many peoples, that method is termed "aki" (to nip with the teeth). (I am indebted to Mrs. Kawena Pukui for these notes.)

Pacific Native Names for Lice

The word "uku (kutu)," meaning louse, is widespread in many Pacific dialects. The following representative list is of interest and shows the continuity of the name over a vast area:

Malay—kutu	Futuna—kutu
Java—kutu	Tonga—kutu
Philippines—katu, cuto	Samoa—'utu
New Britain—utu	Rarotonga—kutu
New Hebrides—gutu, kutu	Tahiti—'utu
Santa Cruz—kutu	Tuamotu—gutu
New Zealand—kutu	Marquesas—kutu
Fiji—kutu	Mangareva—kutu

Parasites: no insect parasites and no effective bacterial, fungal or protozoan parasites are known.

Predators: man alone; but some peoples delouse their vestments by exposing them to ants which may be efficient "delousers."

There is considerable question as to what are the best terms to apply to the forms of *Pediculus humanus*. They might be called "races," "varieties," "forms" or

not named. Ferris (1935:51 [577]) says, "the bulk of the evidence supports clearly the view that these two forms are merely extremes of a single species; that every combination of and intergradation between their characters exists. . . ."

Head lice and body lice may or may not be distinguishable, because of the variability of the characters used to separate them. In general, the antennae of the body louse are longer and more slender than those of the head louse; body lice are, on the average, larger than head lice, and the lateral notches marking the segments of the abdomen may be more clearly defined in head lice. However, these distinctions are variable and are often indistinct and are not to be relied upon entirely. Lice answering the description of head lice may at times be found acting as body lice. The best distinction appears to be in their habits. Head lice usually deposit their eggs on hair, whereas body lice normally lay theirs in clothing. Head lice and body lice can be crossed easily and the offspring remain fertile through succeeding generations. Head lice forced to live on the body will ultimately give rise to generations which have assumed the characteristics of body lice. It is worthy of note, however, that there appear to be certain differences in the genetic make-up of the forms, for it has been reported that the percentage of intersexes rises distinctly in hybrid populations. Detailed genetical studies remain to be undertaken.

Biology: To my knowledge, no biological studies of human lice have been made in Hawaii. The oval, pale-yellowish eggs which are cemented to hairs or fibers of clothing are about 0.3 mm. wide and 0.8 mm. long. In Hawaii they probably hatch in eight to ten days. There are four instars; the nymphs molt thrice. The duration of the nymphal life of the head louse is about eight days, and is somewhat longer for the body louse. On the average, adults live about a month, but may live from one week to more than seven weeks. It is probable that the adults can live only three to five days when separated from their hosts in Hawaii, and the length of life is shortest in hot weather. Copulation may take place a few hours after the adult stage is reached, and egg laying begins about four days after the last molt. The head louse most commonly lays its eggs (called "nits") near the base of hairs behind the ears of its host, but the whole scalp may be affected, and even the eyebrows and eyelashes are at times infested. The body louse may lay its eggs on body hairs, but it most commonly oviposits on underclothing and has a special liking for the region of the nape of the neck. It is most common to find ten or fewer lice on a human head, but there may be hundreds or even a thousand or more present (see Buxton, 1939, for detailed discussion). Among some negligent peoples, individuals may be heavily infested. On some primitive tropical people who wear few clothes, body lice have been reported in abundance from their heads and loin cloths.

Pediculosis (lousiness) is now usually the result of squalor or abnormal crowding of people, at least in Western civilization. The rise in the general standard of living and personal cleanliness has had much to do with the elimination of human lice in modern society. However, lice remain among the most dangerous ectoparasites of man. Many people make little effort to control them, and through their ignorance of disease transmission, are largely unaware of the actual and potential dangers

of being lousy. Wherever there are dirty, unkempt, crowded people whose general level of education and personal hygiene is low, or when times of abnormal stress, poverty and war drastically change the living habits of large and small populations, lousiness usually obtains. Wartime conditions are obviously most conducive to pediculid development and dispersal.

Although pediculosis was at one time prevalent in Hawaii, we do not now hear much more about it than in the better mainland areas of the United States. It used to be a common sight to see people unconcernedly delousing one another in Hawaii. The head louse is not uncommonly found among school children now, and delousing may be on occasion resorted to by school nurses. On occasion, head louse infestations of more than 10 percent have been reported from certain schools in Honolulu. Unfortunately, no general statistics on pediculosis are available in the islands. It is of considerable interest that the body louse is rarely encountered in Hawaii, evidently because of the cleanly habits of most of our people who insist upon frequent baths and fresh, well-laundered, clean clothes. It is noteworthy that it is a tradition among the Japanese always to bathe before going to bed. The scarcity of body lice among the Malayan peoples has been noted by other authors. With World War II came an increase in lousiness among Hawaiian school children—evidently because less attention was given children by “war worker” parents and because of more crowded conditions and inadequate housing.

Medical importance: The reader is referred to the several textbooks on medical entomology and parasitology and to Buxton (1939) for much more extensive discussion and detailed reviews of human lice in relation to disease than will be given here.

In many regions of the world, human lice transmit serious diseases, and although we in Hawaii are most fortunate in not now being plagued by louse-borne disease, it will be worth-while to review these diseases briefly here.

The effect of louse bites on human hosts varies. Some few people hardly notice the feeding of lice, whereas others may be very sensitive. Some rare individuals are immune to louse attack, because lice refuse to feed upon them. However, the feeding of lice usually causes definite reactions. On most people, small, reddish papules appear a few hours after each bite, and these itch and cause much scratching. Sensitive individuals develop a distinct rash. It has been shown that the salivary secretions of the lice have a definite toxic effect on the host. When infestation is heavy, general systemic upsets may occur; there may be fever, adenitis, skin eruptions, anemia, a decided feeling of fatigue, insomnia and irritability. Scratching of the itching bites frequently results in secondary infestations by such micro-organisms as staphylococci and fungi and may lead to extensive dermatitis or impetigo. Some workers have shown that tropical impetigo may be carried from person to person by lice. Individuals with prolonged pediculosis may develop a thickened, roughened, pigmented skin (melanoderma) which has been termed “vagabonds’ disease.” It is of interest to note that experiments with rats show that vitamin B deficiency is conducive to lousiness.

It has been shown that lice may transmit some diseases mechanically. One disease shown to be so transmitted on occasion is bubonic plague. Chandler (1940:533) says, "Lice do not transmit plague by their bites, but may do so when crushed. Natives in Java kill lice by mashing them against the head of the host, which should make infection through the scratched sores on the head very easy. In Ecuador and Peru natives are said to kill lice by crushing them between the teeth; there is much more danger involved when man bites louse than when louse bites man."

Three serious diseases are transmitted by lice: epidemic typhus, trench fever and relapsing fever (epidemic typhus must not be confused with endemic or murine typhus, which is established in Hawaii). Most fortunately, none of these diseases has become established in Hawaii, but it will be worth-while briefly to review them here.

Epidemic typhus is caused by *Rickettsia prowazeki* (rickettsias are considered to be allied to bacteria). It is transmitted from man to man by lice, and is essentially a disease of certain temperate regions. The micro-organisms develop in great numbers in the epithelial cells of the midgut of the louse; the cells eventually rupture and the *Rickettsia* pass out with the louse excreta. Man is not infected through the bite of the louse, but normal infection is caused by scratching the bite and inoculating the abraded skin surface with infected louse feces which are deposited on the skin. It has been shown that the disease organisms will withstand long periods of desiccation in louse excreta, and it is believed that it is possible to acquire the disease through air-borne louse feces. The incubation period in man is about 10 days and the course of the disease is from about 10 days to over three weeks. The mortality rate may be 15 to 75 percent. Herms (1939:111) says, "Wherever human beings are concentrated in close quarters, especially in times of war and famine, this disease may become rampant. The disease is characterized by a high fever, backache, headache, bronchial disturbances, a congested face... a brick-red mottled eruption which later spreads, forming brownish irregular blotches."

Buxton (1939:66) presents a graph that shows a remarkable and rapid reduction of the disease from a few thousand deaths in England in 1870 to none in the years 1919 to 1937. He attributes this disappearance to the reduction of pediculosis. Riley and Johannsen (1932:132) note that

Until 1870 the disease was endemic and in some cases even prevalent in most of the countries of Europe, but from that period until the World War it was almost unnoted. The crowding of soldiers and prisoners of war and the movements of great masses of homeless people under insanitary conditions furnished again ideal conditions for the development of the disease, and its ravages constituted the major sanitary problem of the time. It is established that during the war over 10,000,000 Russians had typhus and that of these over 2,000,000 died. In April of 1915 it was reported that Serbians were dying at the rate of 9,000 per day. Medical men and nurses were no more exempt than was the general populace. Out of 460 Serbian doctors 360 were attacked during this outbreak and more than 120 died. In Poland conditions were even worse....

Trench fever is also caused by a *Rickettsia*, but instead of the causative organism (*Rickettsia quintana* [*R. pediculi*]) developing intracellularly in the louse intestine,

it multiplies in the lumen of the midgut. "This disease was so common during World War I as to cause more sickness than any other disease except scabies, though it was a relatively mild disease. Before the war it was unknown, and it has fallen into complete obscurity since then." (Chandler, 1940:214.) The transmission of the disease is accomplished by scratching the disease organisms from louse feces into the skin. For detailed studies of this disease, see R. P. Strong et al., 1918, and David Bruce, 1921.

Relapsing fevers are transmitted to man by ticks or lice. Epidemic relapsing fever is caused by spirochaetes; the louse-borne types are strains of *Spirochaeta recurrentis*. The epidemic louse-borne type is more important than the "sporadic" or tick-borne type. After a blood meal by the louse, the spirochaetes pass through the intestines and multiply in the haemocoel of the louse. They do not escape from the haemocoel via the rostrum or salivary secretions and are not passed out with the feces. It is, therefore, necessary that a louse or lice be crushed on one's person and the spirochaetes inoculated into an abrasion or mucous membrane before the disease can be transmitted from louse to man. At present the louse-borne form of the disease appears to be absent from North America, western Europe, and Oceania, but present in Central and South America, North Africa, eastern Europe, and Asia.

Control of human lice: Lice are spread by contact, and a knowledge of their habits and methods of dispersal will aid greatly in their control. Fortunately for us in Hawaii, the body louse is rarely encountered. The promiscuous use of head-gear, combs, brushes and clothing invites lousiness, even here in Hawaii. Those who may have to deal with large-scale delousing projects are referred to the standard textbooks and technical reports for detailed control procedure, and we may briefly outline suggested control measures for Hawaii. Control begins with cleanliness, and all lousy individuals should be given initial, thorough bathings and their clothes washed or fumigated.

The use of 10 percent DDT dust gave spectacular control of lice in recent applications in war areas, and its use may become more general in the postwar period. It is dusted into the hair of the infested individual and applied generously to underclothing. Its use may replace most of the following control methods.

Control of head lice in males can be facilitated by cutting the hair short or by shaving the head when such a procedure is indicated. However, in our society the stigma carried by one whose head has been shaved because of pediculosis must be considered.

Trembley (1943:795) highly recommends the use of derris, and says, "Derris is an effective material for combating the head louse... and the pubic louse... The application of derris powder to louse-infested heads is a practical method of controlling head lice, and if persistently and generally applied should result in eradication [of lice] from a community..." It is suggested that about one teaspoon of finely ground derris containing 3 percent of rotenone be applied with a salt shaker and worked well into the hair, care being taken not to get the powder into the eyes; the hair should not be washed for several days following treatment.

The dusting should be repeated two or three times for effective control, because the dust does not kill the eggs. The material can be used similarly for pubic lice, but too much dust should not be applied, because it causes severe irritation to some people. The dust can be colored so that it will not be conspicuous on blond or brunette hair, thus enabling children to go to school without embarrassment while under treatment.

A new formula showing much promise has been brought to attention recently. It consists of an emulsion of 5 percent isobornyl thiocynoacetate and 0.6 percent dioctyl sodium sulfosuccinate. About two ounces of the fluid are lathered into the hair and left for five or ten minutes; the hair is then combed and allowed to dry. The next day the dried emulsion is washed out with soap and water. The poison irritates the eyes and care should be taken not to get any in the eyes. This treatment kills both eggs and adult lice, and usually control is complete with a single application.

A mixture of equal parts of kerosene and cottonseed oil or olive oil is an effective and simple delousing agent; the hair is thoroughly saturated with the mixture and then enclosed in a bathing cap or a tight towel wrapping and left for several hours. Xylene (xylol) in vaseline (one-quarter xylene in three-quarters vaseline) has been found to be good, but the material may irritate the skin. Another simple method recommended is to saturate the hair with 70 percent ethyl alcohol and to enclose the hair in a bathing cap for an hour or more. (Caution: keep in mind the inflammability of the materials used!) After these treatments, the hair should be washed well with warm, soapy water. Careful and thorough use of a fine-tooth comb is also recommended.

When infestations of body lice are encountered, the following procedure might be followed: Remove all clothing and have it thoroughly washed and ironed or dry-cleaned and pressed; treat bedclothing, towels, etc., similarly. It is recommended that all infested or possibly infested material be fumigated before laundering. Clothes may be fumigated at home by placing them in a tight box, can or bin and scattering ample amounts of naphthalene (mothball) flakes or paradichlorobenzene crystals among the clothing and leaving tightly closed for a day or more. Carbon tetrachloride (sold under such trade names as "Carbona," etc., and used in certain types of fire extinguishers) is an adequate fumigant which is cheap, non-explosive and simple to use. However, very hot water will kill all lice and eggs instantly. Exposure to direct sunlight on hot days will usually kill the lice in clothing if it is spread out well. It may be advisable to treat rooms in which heavily infested people have lived. Probably a simple closing of the rooms for about three weeks in Hawaii will result in the death of all the lice. Proper fumigation is recommended, but fumigation is often not feasible or possible. If methyl-bromide or cyanide fumigation is impossible, carbon tetrachloride might be used. Latta and Yeomans (1943:402) outline methods and equipment used for methyl-bromide fumigation of clothing infested by lice. Buxton (1939:90) recommends spraying the floors and walls of infested rooms with a kerosene emulsion made as follows: dissolve three parts by weight of soft soap in 15 parts water; while agitating the

liquid, add kerosene until no more will emulsify. This concentrate can be stored and used as a spray diluted one part to 20 parts of water.

It must be remembered that satisfactory control cannot be attained unless the source of lice infestation is destroyed. It does no long-term good to delouse children at school, only to have them become reinfested in their own homes. Physicians and public health nurses should follow up infestations and try their best to apply control where it will do the most good.

Subfamily PHTHIRINAE

Phthiridae Ewing, 1929:132.

Phthiriidae Brues and Melander, 1932.

This group has been considered by many authors to belong to the true Pediculidae, and they have not separated the genus from *Pediculus* by any suprageneric ranking. Ewing in 1929, however, established the new family Phthiridae (not Phthiriidae) for the crab louse principally because of the fusion of the abdominal segments and the presence of lateral abdominal tubercle-like processes. Ferris (1935:77) says, "Ewing has placed it (*Phthirus*) in a family, Phthiriidae, (Phthiridae) by itself. While it is indeed a peculiar genus, such a separation seems to remove it unnecessarily far from its relatives, which are evidently among the other Primate-infesting forms." The opinions of each author bear weight. I feel that perhaps a compromise between the two opinions is justified, and I am, therefore, placing the genus *Phthirus* in the Phthirinae—a subfamily of the Pediculidae.

This group contains one genus, which in turn is monotypic or may contain a second species.

Genus **PHTHIRUS** Leach, 1815

Phthirus, of authors.

This genus contains one well-known ectoparasite of man and an imperfectly known "species" described from eggs and first-stage nymphs from the Belgian Congo from *Gorilla berengeri*.

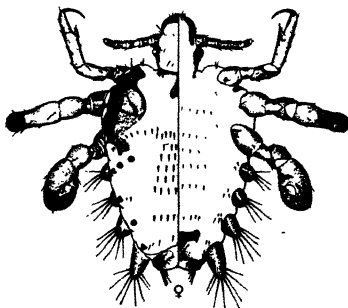


Figure 177—*Phthirus pubis* (Linnaeus), the crab louse. (After Ferris, 1935.)

***Phthirus pubis* (Linnaeus) (fig. 177).**

Pediculus Pubis Linnaeus, 1758:611.

Phthirus inguinalis Leach, 1815:77 (Edinburgh Encyclopaedia, vol. 9. I have not checked this reference).

For detailed synonymy, illustrations, descriptions and discussion, see Ferris, 1935:77-82, figs. 335-337.

Genotype of *Phthirus*.

The pubic louse, crab louse; Hawaiian name: "uku-papa."

Immigrant. Cosmopolitan. Probably imported to the Hawaiian Islands by early European voyagers, but not present in old Hawaii.

This louse cannot be confused with any other; its shape alone is diagnostic. It is much less common than *Pediculus*, but perhaps it may come to the attention of local physicians more often than *Pediculus* because of the position it occupies on its host.

Biology: Much less work has been done on the life history and habits of the crab louse than on the body and head lice. Man is the only host upon which the louse is known to be able to breed successfully. The eggs are glued only to hairs, and they have an incubation period of six to eight days. The adult stage is reached in 13 to 17 days after eclosion. Nuttall found the egg-to-egg history to take 22 to 27 days. The mature lice are thought to live not more than a month, and larvae and adults die within a day or two after removal from the host. The adults are quite sedentary and may cling to the same hairs and feed continuously for long periods of time. The lice are most commonly found in the pubic and peri-anal area, but no part of the body is absolutely exempt from attack. Although the heads of infants may become infested, crab lice are rarely found on the heads of adults. Reports of individuals infested from ankles to eyebrows are on record. Occasionally the eyelashes may be heavily infested.

The reactions of persons to the bites of the crab louse vary, as do man's reactions to *Pediculus*. The feeding of the lice usually causes a decided itching, with subsequent severe scratching which may lead to secondary infections. The salivary products of the louse cause a bluish discoloration of the tissue. "The 'blue spots' ... are 0.2 mm. to 3.0 cm. in diameter, with an irregular outline. They are painless, do not disappear on pressure, and appear to be in the deeper tissues. They appear some hours after the crab louse has bitten and last for a number of days. They do not invariably follow the bite of this insect, but when they develop they are characteristic of *Phthirus*, not *Pediculus*..." Buxton, 1939:97 (after Nuttall, 1918).

Hermes (1939:107) calls infestation by *Phthirus* "phthiriasis"; "pubic pediculosis" is also used.

The role played in the transmission of disease by this louse is unknown, but it does not appear to be an important vector.

The most common method of transmission of the crab louse appears to be through sexual intercourse. But it may be transmitted in other ways. Many victims are infested from toilet seats and occasionally from bedding or simply from contact with infested clothing or individuals.

Control: 10 percent DDT dust is an efficient insecticide. The clipping or shaving of the hair in the infested areas is usually recommended, but this may lead to irritation to such active persons as soldiers during wartime. The xylene ointment described under *Pediculus* is recommended. Derris powder has been found effective, but some people may be irritated by it. Mercury compounds should be avoided; they are dangerous and are not good insecticides. When the eyelashes are infested, a local anesthetic may be applied and the lice picked off individually by the use of forceps. Thorough washing with hot, soapy water is always indicated for every infestation and following every treatment.

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Because of the overlapping of many of the references listed, it was thought best to combine the bibliographies of the biting and sucking lice.

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Order Odonata Fabricius, 1793

(Odonata is thought to be an abbreviation of Odontognatha; *odous*, a tooth, and *gnathos*, a jaw, thus referring to the toothed maxillae)

Dragonflies, Damselflies

(Hawaiian names: "pinao"; "pinao-ula")

Head hypognathous, large, exposed, free, globular or dumbbell shaped, highly mobile, attached to a very slender neck; labrum large; mandibles strongly developed, fitted for biting and chewing, with well-developed incisor and molar teeth; maxillae with unsegmented palpi; internal lobe, or mala, strongly and conspicuously toothed; labium peculiarly evolved, mentum with two side pieces (*squamae* or *squames*) representing the palpigera, palpi two-segmented, the proximal segment broad, terminating in a hook-like lobe, the distal segment hook-like and movable in all forms excepting the Libellulidae, in which group it and the hook of the proximal segment are lacking; compound eyes very large; three ocelli always present; antennae shorter than head, fused to form a peculiar pterothorax which is inclined backward with the leg position shifted cephalad, the wing position caudad, terga reduced, pleura greatly developed, anterior part of mesothorax which appears to be the dorsum, really formed by the peculiarly extended mesepisterna; legs fitted for grasping and climbing, but not well-fitted for walking, grouped close under the head where they aid in capturing, holding and transferring food to the mouth, trochanters divided into two parts, tarsi three-segmented, claws paired, usually toothed, empodium vestigial; four large, well-developed wings always present, subequal in size, usually held either horizontally at right angles to body or folded vertically above abdomen, complexly net-veined, membrane bare, stiff. Abdomen slender, greatly elongate, 10 complete segments visible, segments 11 and 12 rudimentary, cerci (called superior anal appendages) well developed; ovipositor primitive, present in all Zygoptera, but absent in some Anisoptera; gonopore of male situated on segment nine, but functional penis and accessory organs peculiarly located on segment two. Metamorphosis gradual, incomplete; eggs oblong or ovate and dropped free in water (exophytic oviposition) or elongated and inserted in plant tissues by use of well-developed ovipositor (endophytic oviposition), some non-Hawaiian forms insert their eggs in mud; larvae, called naiads or nymphs, aquatic with a few endemic exceptions, all predaceous; the number of instars is stated to be between 11 and 15.

The oldest fossil species known have been described from Lower Permian rocks. Some of the ancient forms (Carboniferous) had wing expanses of more than two feet. There are now about 3,500 described living species. The order is cosmopolitan, with the greatest modern development in the Neotropical Region. Most of the species are diurnal heliophiles as adults, but some Indo-Pacific and American forms are crepuscular or nocturnal.

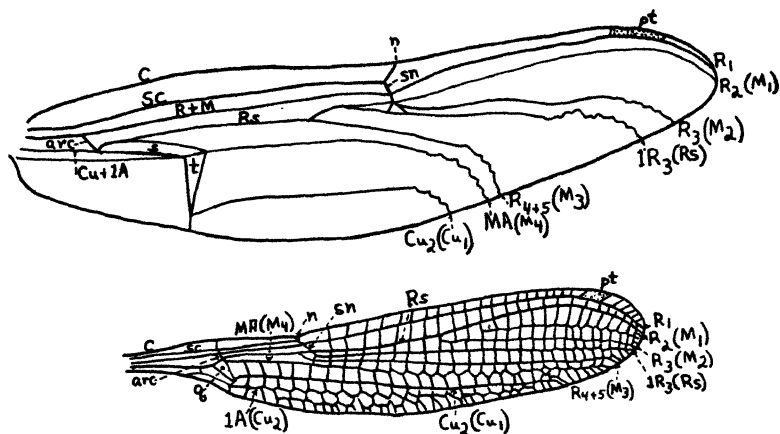


Figure 178—Wing venation of Odonata. Upper figure is the fore wing of a dragonfly (Anisoptera) with the cross-veins omitted to show the principal veins. The lower figure is of a *Megalagrion* damselfly (Zygoptera). The nomenclature is based upon that of Tillyard with an alternate system in parentheses. 1A, first anal; arc, arculus; C, costa; Cu+1A, cubito-anal; Cu₂, second cubitus; MA, anterior median; n, nodus; q, quadrangle; pt, pterostigma; R₁, radius (main stem); R+M, radio-medial; Rs, radial sector; R₂, R₃, 1R₃, R₄₊₅, all branches of radial sector; s, supratringle; sc, subcosta; sn, subnodus; t, triangle.

The organs and method of copulation are peculiar. In fact, they are unique among animals. The genital pore of the male is situated on the ninth abdominal sternite, but the functional intromittent organ is a strange secondary development situated on the venter of the second abdominal segment. When ready to copulate, the male bends his abdomen under and forward and transfers spermatozoa from the gonopore to a vesicle near the "penis" on the second ventrite. During copulation the male grasps the female with his caudal claspers by the top of the thorax, neck or head, and she swings her abdomen forward so that her gonopore comes in contact with the secondary copulatory organ complex of the male. Copulation takes place while on the wing, or settled, and we speak of copulating pairs as "tandems."

The adults of most species capture all their food while on the wing, but some of our species have been observed to pick their prey off plants and the ground. The anteriorly placed, modified legs form a catching basket. The nymphs (which are called "olopelope" in Hawaiian) have a remarkable folding, prehensile labium which can be shot out with great speed to capture prey.

The student is referred to the standard textbooks for more detailed discussions of the order.

There are 34 forms found in Hawaii. Of this total, five are immigrants and 29 are endemic. The native species include a monotypic genus, *Nesogonia*, in the Libellulidae; a geologically recent derivative of the Holarctic *Sympetrum*; a single native species of the cosmopolitan *Anax*; and 27 forms belonging to *Megalagrion*,

an endemic genus derived from, and closely similar to, the Oriental-Pacific *Pseudagrion*.

These data may be compared with the Odonata fauna of Samoa, where 29 forms are found. There we find that the Zygoptera are represented by 13 forms. Three of the Zygoptera are immigrant, one is a *Pseudagrion* and one an *Agriocnemis*. Five of the remaining eight belong to *Ischnura*, while the other three belong to local segregates of *Ischnura* which have been assigned two generic names. Thus, in Samoa, *Ischnura* has a comparable, if less extensive, development to the Hawaiian *Megalagrion*. The Samoan dragonflies are much more numerous than the Hawaiian forms. The Anisoptera are there represented by 16 forms, belonging to 12 genera; two of these forms are thought to be endemic and 14 are immigrants. The proximity of Samoa to Fiji and other island steppingstones to Papua and Australia accounts for the richer generic representation and the high percentage of immigrants.

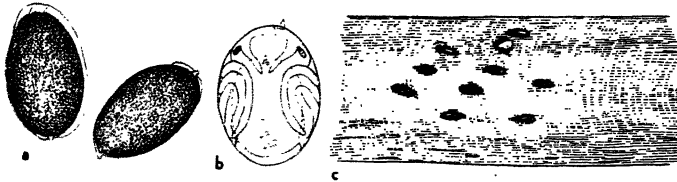


Figure 179—Eggs of Odonata: a, eggs of *Nesogonia blackburni* (McLachlan), which are laid free in water; b, the same, one day before hatching; c, part of a stem of *Herpestes monieria* showing egg punctures and the protruding parts of the shells of hatched eggs of *Anax junius* (Drury). (From drawings by F. X. Williams.)

TABULAR ANALYSIS OF THE HAWAIIAN ODONATA

FAMILY	GENERA	ENDEMIC GENERA	NON-ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Aeshnidae	1	0	1	2	1	1
Libellulidae	3	1	2	3	1	2
Coenagriidae	3	1	2	29	27	2
Totals	7	2	5	34	29	5

Percentage of endemism in native group: genera, 66 $\frac{2}{3}$ percent; species, 100 percent.

Percentage of present-day fauna native: 85 percent.

Percentage of present-day fauna adventive: 14 percent.

Average number of forms per genus in native group: 9.7.

Average number of forms per genus in adventive group: 1.

KEY TO THE SUBORDERS OF ODONATA FOUND IN HAWAII

1. Adults 2
- Larvae 3

- 2(1). Wings held open and horizontal when at rest, hind pair broader near base than fore pair; eyes very large and touching or almost touching on top of head. **Anisoptera.**
 Wings held vertical and close together over back when at rest, hind pair not broader near base than fore pair; eyes widely separated above. **Zygoptera.**
- 3(1). Gills enclosed in rectum, not externally visible; swim by squirting water from anus ("jet propulsion") **Anisoptera.**
 Gills caudal and external, plainly visible; swim by wriggling and sculling with gills. **Zygoptera.**

Suborder ANISOPTERA Selys-Longchamps, 1834

Dragonflies

(Hawaiian name: "pinao")

Wings held horizontally or depressed in repose; hind wing always more or less considerably broader than fore wing near base; radius branched, radial sector crossing two branches of media; oblique vein and bridge present; discoidal cell differentiated into triangle and supertriangle. Eyes large, often meeting mid-dorsally, never separated by a space greater than their own diameter. Labium variable. Male with two superior and one inferior anal appendages, all placed dorsally above anus (the inferior may be bifid or trifid); penis jointed; female with superior appendages but no inferior appendage, ovipositor variable. Larvae with gills in rectum (proctobranchiate); anus closed by an anal pyramid formed of three spines, one medio-dorsal and two lateral; gizzard with four to eight dental folds. (Modified from Tillyard, 1917:259.)

Of the two suborders of Odonata, this is the least developed in the islands. There are five species representing four genera here, but only two of these are endemic, and these two species are geologically recent derivatives of widespread genera or species.

The dragonflies are much more active and much faster fliers than the damselflies. The adults of all our species emerge from their nymphal cases in the morning hours.

KEY TO THE SUPERFAMILIES OF ANISOPTERA

1. Adults 2
 Naiads 3
- 2(1). Triangles of both fore and hind wings equidistant from arculus **Aeshnoidea.**
 Triangles of hind wings nearer arculus than those of fore wings **Libelluloidea.**
- 3(1). Labium flat, not concealing face; lateral lobes curved, mandible-like **Aeshnoidea.**
 Labium spoon-shaped, covering most of face (up to antennae); lateral lobes subtriangular and fitting close against sides of apex. **Libelluloidea.**

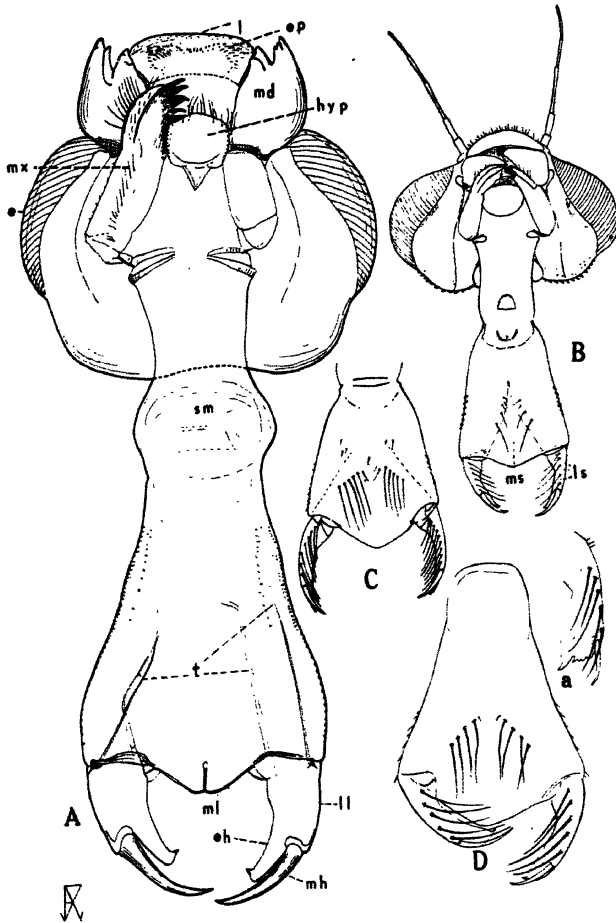


Figure 180—Cephalic details of some Odonata naiads. **A**, *Anax strenuus* Hagen, underside of head with "mask" unfolded, left maxilla removed: **a**, eye; **eh**, end hook; **ep**, epipharynx; **hyp**, hypopharynx; **l**, labrum; **ll**, lateral lobe; **m**, mentum; **md**, mandible; **mh**, movable hook; **ml**, median lobe; **mx**, right maxilla; **t**, tendons; **sm**, submentum. **B**, *Megalagrion leptodemas* (Perkins), underside of head with labrum unfolded: **ms**, median setae of median lobe; **ls**, setae of lateral lobe. **C**, *Megalagrion xanthomelas* (Selys-Longchamps), inner view of mentum of "mask." **D**, The same of *Enallagma civile* (Hagen): **a**, inner face of lateral lobe. (Rearranged from original figures for Williams, 1936.)

Superfamily AESHNOIDEA Selys-Longchamps, 1840

Family AESHNIDAE Burmeister, 1839

The Darners

Opinion Number 34, rendered by the International Committee of Zoological Nomenclature reads: "Aeschna vs. Aeshna.—Since evidence of derivation of the word is not contained in the original publication, the original spelling of Aeshna should be preserved." Therefore, the spelling *Aeshna* is used here.

Subfamily AESHNINAE

Tribe AESHNINI

Genus ANAX Leach, 1815

This genus contains some of the largest of all living Odonata. The largest dragonfly of North America is an *Anax*, and the native Hawaiian *Anax strenuus* is not only the largest Hawaiian dragonfly, but is also larger than the largest North American species (*A. walsinghami* from California).

KEY TO THE SPECIES OF ANAX FOUND IN HAWAII

1. Costal margins of wings yellowish brown, comparatively pale
.....**junius** (Drury).
2. Costal margins of wings blackish brown, comparatively dark
.....**strenuus** Hagen.

These two species are closely allied. Perkins (1913:clxxv) says that he has taken the males of one of these species coupled with the females of the other, and "captured three such pairs in the course of two days, when collecting in the mountains near Waialua on Oahu. Owing to the peculiar method of copulation in dragon-flies, it is not possible to say whether this truly took place or not." The nymphs are closely similar to one another.

Anax junius (Drury) (figs. 179, c; 181; 182; 183; 187, a-c).

Libellula junia Drury, 1770:112, pl. 47, fig. 5.

Warren, 1913:72, food habits. Needham and Heywood, 1929:129, fig., good general notes on habits. Kennedy, 1934:354, figs. 17, 18, 21, 23, 24. Williams, 1936:287, figs. 41, 42, 50, 51, bionomics.

The common green darter.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii.

Immigrant(?). Widespread in the Northern Hemisphere. A common pond species in the Americas (type locality: New York). This species was first recorded from

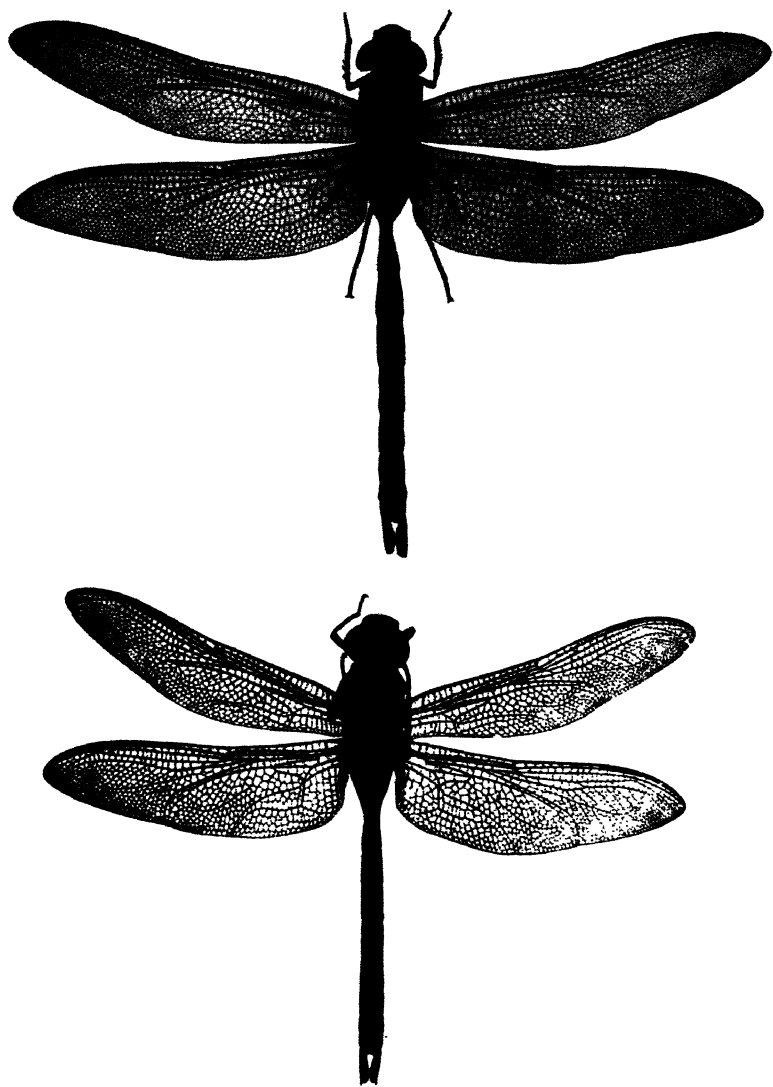


Figure 181—*Anax strenuus* Hagen, male, top, expanse 5 inches; *Anax junius* (Drury), male, bottom, expanse $4\frac{1}{8}$ inches.

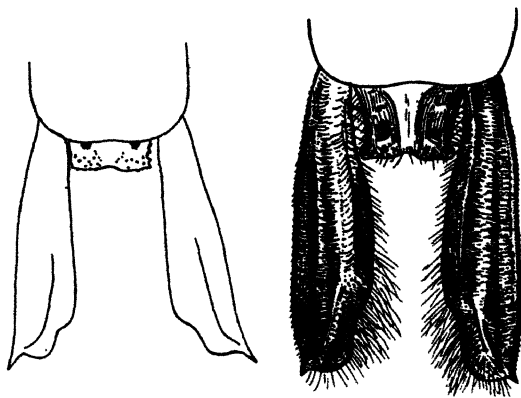


Figure 182—Dorsal views of male terminalia of *Anax junius* (Drury), left, and *Anax strenuus* Hagen, right. (After Williams, 1936.)

the islands by Hagen in 1867 (under the synonymous names of *A. severus* and *A. ocellatus*). There are no definite earlier data regarding this species in the Territory, but, because of its ability to find its way to distant parts of the world, I feel inclined to consider that perhaps it should be called "indigenous." It may have been in Hawaii for several hundred years as a natural immigrant from North America.

Parasite: although none has yet been recorded in Hawaii, it is possible that the species of *Anagrus* (?) which attacks the eggs of *Anax strenuus* may also parasitize the eggs of this dragonfly.

Predators (of naiads): fish, especially top minnows, frogs, other odonate larvae.

This species closely resembles the native *Anax strenuus*. It averages about 25 mm. less in expanse and has more yellowish wings. Williams (1936:287-288) says,

The male *junius* has the head, thorax and first segment of the abdomen green, the remainder of the abdomen being pale blue and black. The female has the greenish extending to include the second segment of the abdomen, the slender remainder being chiefly a gray brown above with green on the sides of the few terminal segments. Specimens of this dragonfly that have a wing expanse of 114 millimeters are considered large individuals though not uncommon, while those measuring 110-112 millimeters are frequently met with, and hence it would appear that these Island representatives are of a generally greater size than the same species on the mainland where Needham and Heywood (1929) give its wing expanse as 105 mm., and Seeman (1927) as 107 mm.

Williams records a specimen from Oahu which had a wing expanse of 117 mm.

This species is characteristic of the lowlands, but it is often found high in the mountains and has been seen at more than 13,000 feet. It breeds in lily ponds, reservoirs, fish ponds, swampy areas and ponds, rice fields, taro fields, etc. Williams (1936:288) notes that it breeds even in brackish water, but it thrives best "Where our lowland bodies of water contain no fish, but teem with such minute

Crustacea as Ostracoda, and with bloodworms, *Chironomus hawaiiensis*, the nymph of *Pantala flavescens* and *Megalagrion xanthomelas*, our lowland damselfly...." Warren (1915) studied the food habits of this species at Honolulu. He found that the larvae ate almost all available insects, crustaceans, molluscs and worms. Blood worms, larvae of Chironomidae, and ostracod crustaceans made up the bulk of the food taken by the nymphs examined by Warren. The larger larvae also eat tadpoles and even small fish. They may become a nuisance in fresh-water fish ponds. The adults feed on a variety of insects including other dragonflies and damselflies, Hemiptera, Lepidoptera, Coleoptera, Diptera and Hymenoptera. They are fond of honey bees.

The following notes on the life history are extracted from Williams' excellent account of the species (1936:287-290). The amber-yellow eggs are about two mm. long. They are inserted into the tissues of submerged plant stems, such as *Marsilea* and *Commelina*. The nymphal period is much shorter in Hawaii than on the mainland where it is said to last about a year, but the duration of the life cycle has not been definitely ascertained in the islands. "The nymph of *Anax junius*



Figure 183—Egg punctures of *Anax junius* (Drury) in a *Nymphaea* leaf. Photograph by F. X. Williams.)

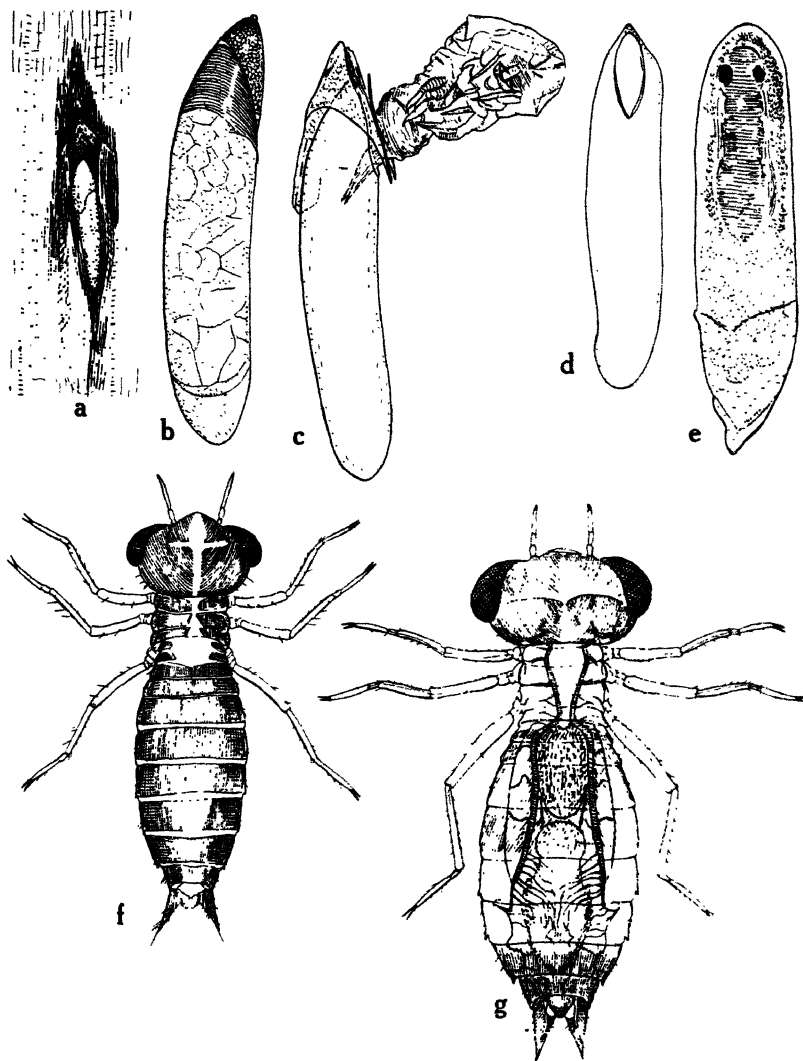


Figure 184—Developmental stages of *Anax strenuus* Hagen: a, eggs inserted in stem of *Commelina nudiflora*; b, side view of egg; c, hatched egg showing cast exuvium of pronymph protruding; d, egg shell showing exit hole; e, egg parasitized by an *Anagrus* wasp, with the parasite showing through; f, naiad (about 2.6 mm. long) after emerging from pronymphal skin 3 mm. long; g, next stage naiad (about 3 mm. long), the respiratory system is well shown here. The branchial basket lies in the pale abdominal band; the oval area just behind the thorax is the remains of the yolk in the midgut. (From original drawings for Williams, 1936.)

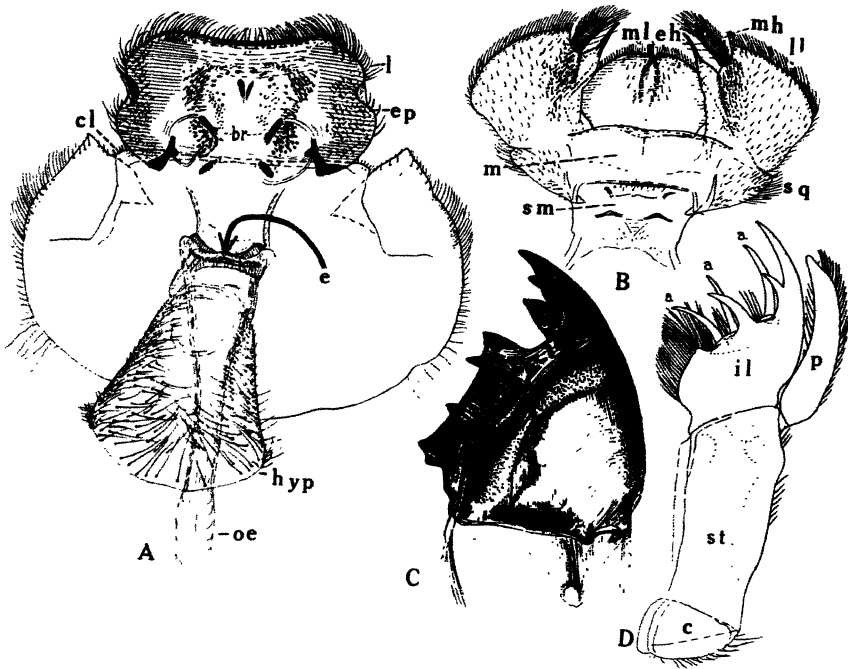


Figure 185—Morphological details of the mouth parts of the adult of *Anax strenuus* Hagen. A, underside of front part of head: l, labrum; ep, epipharynx; br, hair brushes (taste organs?); cl, lower corner of clypeus; hyp, hypopharynx, bent back to expose entrance to oesophagus (oe), at e. B, Labium: sm, submentum; m, mentum; ml, median lobe; eh, end hook; mh, movable hook; ll, lateral lobe; sq, squama. C, Right mandible. D, Maxilla: c, cardo; st, stipes; il, inner lobe; p, palpus; a, a, a, movable teeth. (From Williams' original drawings, 1936.)

undergoes many molts. In its early life it is conspicuously bicolorous...pale yellowish and dark brown; later it is brownish, more or less striped with green and is flecked with darker spots, etc. It is then somewhat more definitely patterned and less dusky than the nymph of *Anax strenuus*, that dwells in generally more shady situations in the uplands. The full grown nymph of *junius* is about 45 millimeters long. The adult issues under cover of darkness."

Anax strenuus Hagen (figs. 180, A; 181; 182; 184, a-g; 185, A-D; 186, a).

Anax strenuus Hagen, 1867:34. Blackburn, 1884:413, male. Kennedy, 1934:356, figs. 16, 22, 25, 26. Williams, 1936:274, figs. 39, 40, 43, 44-49. 52-57.

The giant Hawaiian dragonfly.

Endemic. Kauai, Oahu (type locality), Molokai, Lanai, Maui, Hawaii. (McLachlan, 1883:231, says, "The type is a female taken during the Danish 'Galathea' expedition, and is in the Copenhagen Museum.")

Parasites: an unidentified *Anagrus* (?) (Hymenoptera: Mymaridae) attacks the eggs. Dr. Williams tells me that it is evidently not *Anagrus insularis* Dozier, which attacks damselfly eggs here. Adults are occasionally seen with many mites attached to their abdomens.

Predators (of naiads): fish, *Gambusia* top minnows, gobies and others; other naiads; water beetles and their larvae.

This is not only the largest Hawaiian dragonfly, but it is also the largest Hawaiian insect. It is larger than any North American species of Odonata. Kennedy (1934:356) says, "It is so similar in color and structure to *Anax junius* which is the only other *Anax* occurring in the Islands that it is sometimes spoken of as a giant *junius*. The writer has wondered if *strenuus* might not be a tetraploid or other polyploid mutant of *junius*." The largest specimen in the Bishop Museum

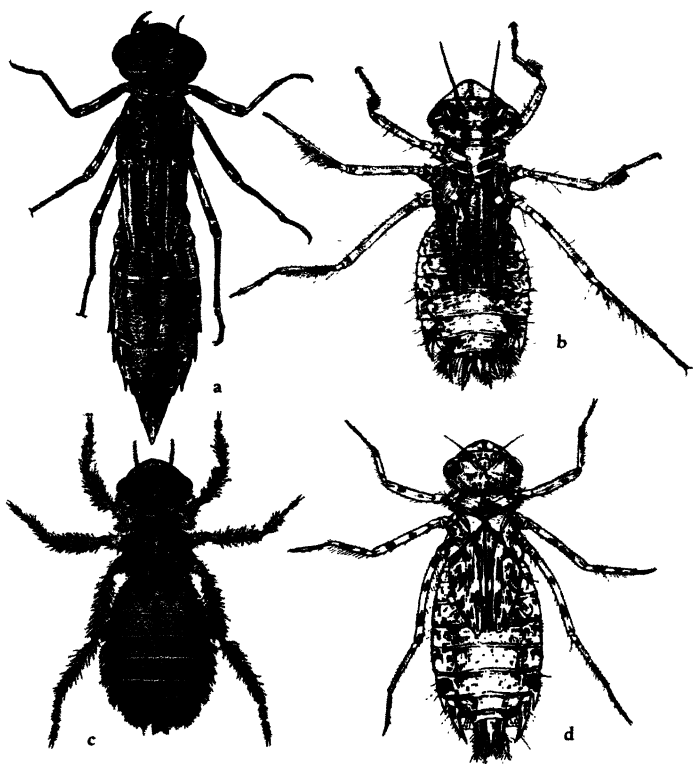


Figure 186—Dragonfly naiads: a, *Anax strenuus* Hagen, a day and a half before adult emerged (54 mm. long); b, *Tramea lacerata* Hagen, full-grown naiad, about 27 mm. long; c, *Nesogonia blackburni* (McLachlan), three-quarters grown (the fuzzy appearance is caused by a growth of *Vorticella* protozoans and bacteria among the hairs); d, *Pantala flavescens* (Fabricius), full grown, about 25 mm. long. (Rearranged from Williams' original drawings.)

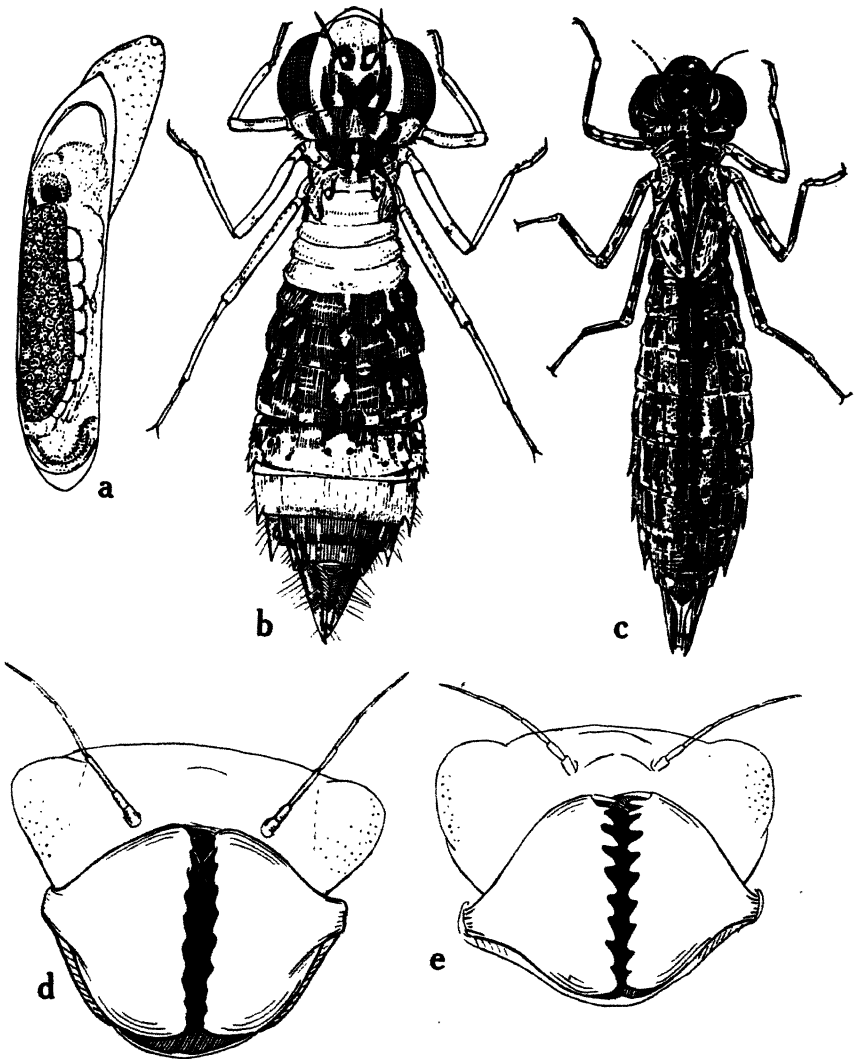


Figure 187—Features of some Odonata: a, egg of *Anax junius* (Drury); b, young naiad of same (12 mm. long); c, a naiad of the same species about three-fourths grown (35 mm. long); d, face of mature naiad of *Tramea lacerata* Hagen; e, face of *Pantala flavescens* (Fabricius). Note differences in size of teeth in lateral lobes. (From original drawings for Williams, 1936.)

has an expanse of 143 mm. Its larger size and general coloration, especially the dark fore margins of the wings, serve to distinguish it from *A. junius*. However, there are differences in the terminalia and the sternites of the first two abdominal segments of the male. These structures are subject to some variation and may be somewhat confusing, but when examined and evaluated by an experienced person, they are of definite value in separating the species. It appears to me that one of the more obvious characters of the male genitalia useful in separating *A. strenuus* from *A. junius* is the shape and size of the "inferior appendage." As indicated in the illustrations, this process is larger on *A. strenuus* and extends distinctly farther caudad than it does on *A. junius*. Its posterior margin is more deeply emarginate, and the postero-lateral angles are more strongly produced than they are in *A. junius*. In life the male may be distinguished easily from the female because of the blue color of its basal abdominal segments.

Whereas *A. junius* is more characteristic of the lowlands, *A. strenuus* is mostly a mountain species and is now only occasionally seen in the lowlands, and then only in certain places. It seems to prefer the deep canyons and cool stream pools of the mountains and breeds up to 6,000 feet or more. In the highlands of Kauai, I have seen the adults flying close to the ground over a grassy, semi-swamp, expertly flushing small moths. They eat a great variety of flying insects, including our large native damselflies.

Williams (1936:274, which reference should be consulted for details) has published an excellent account of the bionomics of this species, and the following notes are abstracted from his careful observations. The females insert their eggs, usually in double rows, into the underwater tissues of *Commelina nudiflora*, *Colocasia* spp. (taro), or other plants growing in the water or partially submerged, or even in pieces of dead, soggy vegetation lying in the water. The incubation period of the eggs, which are 2.0 to 2.25 mm. long, has not yet been accurately ascertained, but it is less than two weeks. The first instar lasts only a few seconds, and then follows a series of molts up to the last or fifteenth instar. Williams found the tarsi to be single-segmented in the first two instars, two-segmented from instar three to seven, and three-segmented from instar eight to 15. The antennae are three-segmented on hatching, four-segmented at instars three to six, five-segmented from instar seven to nine and seven-segmented from instar 10 to 15. The wing pads appear at the fifth instar. A specimen reared from egg to adult by Williams measured 2.6 mm. in length in the second instar and 53 mm. at instar 15. The naiads are brown marked with yellow in the first half of the cycle, but they become more drab in later life. The egg and larval period occupies five to six months.

The voracious larvae are known to eat a variety of organisms among which are earthworms, damselfly and dragonfly naiads (even their own relatives), fly larvae (Chironomidae, etc.), *Hydrobius* beetle larvae (Hydrophilidae), crustaceans such as shrimps, sowbugs, and amphipods, molluscs such as *Physa*, *Lymnaea* and *Melania* ("The smaller shells may be swallowed entirely but larger ones are broken up in its jaws with quite an audible gritty crunch." Williams, 1936:281), tadpoles, small fish, and almost any available insect that happens to fall into the water.

Superfamily LIBELLULOIDEA Selys-Longchamps, 1840

Family LIBELLULIDAE Stephens, 1836

Subfamily LIBELLULINAE

The Common Skimmers

KEY TO THE GENERA FOUND IN HAWAII

1. Adults 2
 Naiads 4
- 2(1). Wings subequal in size, hind wing only slightly broader than fore wing; thorax dark with conspicuous pale maculae **Nesogonia** Kirby.
 Hind wings conspicuously broader than fore wings, fully one-third broader at base than broadest part of fore wings; thorax not so marked 3
- 3(2). Vein R_s in both pairs of wings conspicuously undulated; bases of hind wings with at most a yellowish tinge **Pantala** Hagen.
 Vein R_s in both pairs of wings arcuate but not undulate; bases of hind wings with a large, conspicuous, irregular, dark macula **Tramea** Hagen.
- 4(1). Lateral spine-like projections at posterior angles of last two complete abdominal segments very short, as in figure 186, c **Nesogonia** Kirby.
 Postero-lateral spines on last two complete abdominal segments long and conspicuous, as in figure 186, b, d 5
- 5(4). Teeth on lateral lobes of labium acute, strongly developed **Pantala** Hagen.
 Teeth on lateral lobes of labium low, obtuse, obscure **Tramea** Hagen.

Genus NESOGONIA Kirby, 1898:347

Kennedy, in his paper on the "Origin of the Hawaiian Odonata Fauna" (1929: 979), says, "*Nesogonia* is so close to the holarctic genus *Sympetrum* of fifty or more species that it could be put in that genus with little argument. We do not know *Sympetrum* well enough to say whether *Nesogonia* came from North America or Eurasia." If it is true that our *Nesogonia* is so close to *Sympetrum*, then I feel that much more would be gained by considering our species as a distinct and isolated species of *Sympetrum*, thus clearly indicating its obvious origin and natural affinities, than to maintain it as a monotypic genus of dubious standing. However, I cannot speak with any authority on problems concerning Odonata, and in view of the fact that specialists in the field have continued to use *Nesogonia*, it will remain for future students to consider the correct position of our species. A genus, in my opinion, cannot be maintained on the basis of geographical location alone; it must be morphologically distinct.

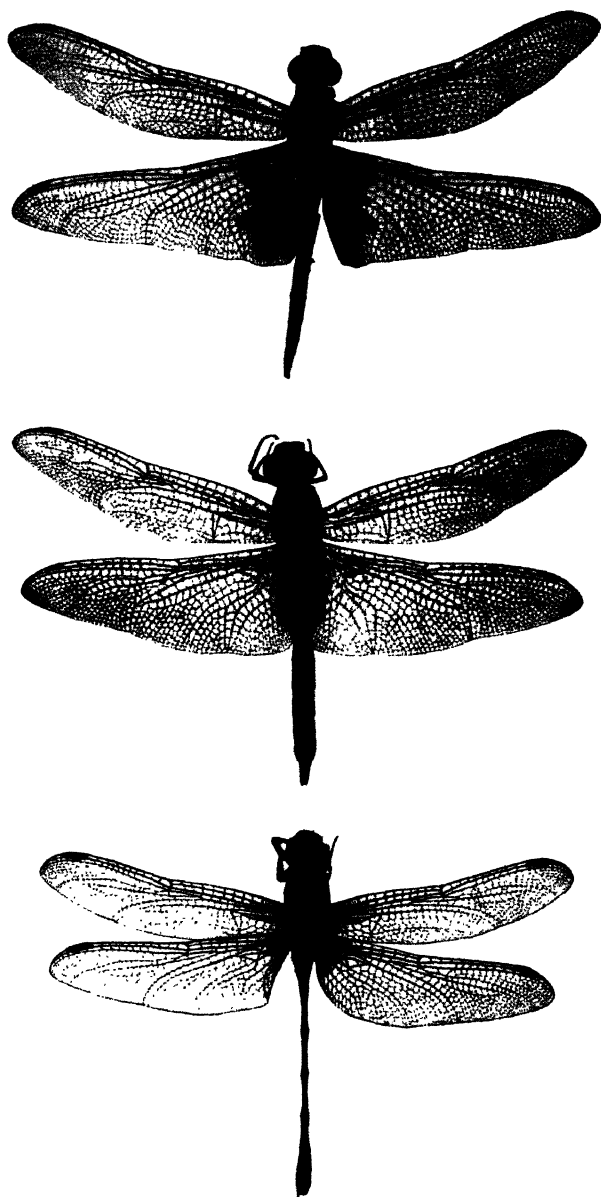


Figure 188—*Tamea lacerata* Hagen, the raggedy skimmer, female, expanse $3\frac{3}{8}$ inches, top; *Pantala flavescens* (Fabricius), the globe skimmer, female, expanse $3\frac{1}{2}$ inches, middle; *Nesogonia blackburni* (McLachlan), Blackburn's dragonfly, male, expanse $3\frac{1}{4}$ inches, bottom.

Nesogonia blackburni (McLachlan) (figs. 179, a, b; 186, c; 188; 189, a-c; 190, a-d).

Lepthemis blackburni McLachlan, 1883:229; 1892:177.

Orthetrum blackburni (McLachlan) Kirby, 1890:36.

Sympetrum blackburni (McLachlan) Karsch, 1890:373.

Nesogonia blackburni (McLachlan) Kirby, 1898:347.

Williams, 1936:290-295, figs. 1-3, 58-65; bionomics.

Blackburn's dragonfly.

Endemic. Kauai, Oahu, Molokai, Lanai, Maui, Hawaii. No type locality was given by McLachlan.

This is a widespread, variable, native denizen of the mountains and native forests. Our smallest dragonfly, it

has an expanse of wing from somewhat less than 3 to about $3\frac{1}{2}$ inches. The wings are for the most part nearly transparent, but the stigmal spot is reddish brown, while at their narrowed base there is a little yellowish brown and just before which, at their articulation with the thorax, there is a bit of red. The body is mainly dark, almost blackish, with some yellowish or greenish yellow dashes on the thorax, a suffusion of reddish at the bulbous base of the abdomen and a long spot of that color towards its slightly clubbed extremity. (Williams, 1936:291-292.)

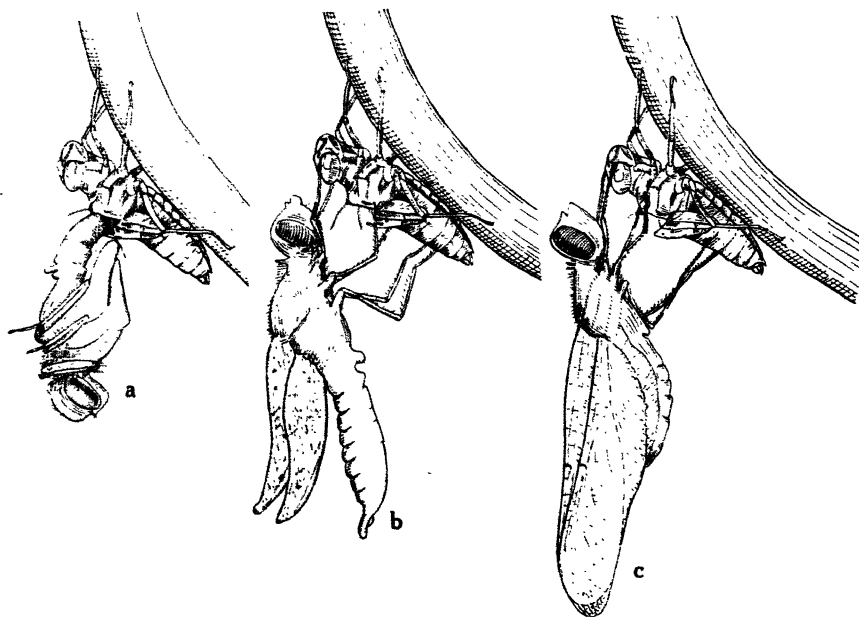


Figure 189—Sketches of stages in the emergence of an adult of *Nesogonia blackburni* (McLachlan) from its nymphal shell. b, 25 minutes after a; c, 15 minutes after b. (From drawings by Williams, 1936.)

Williams (1936:290-295) has published the only account of the bionomics of this species, from which the following details were obtained. The pale, translucent, yellow eggs measure about 0.54 mm. in length and 0.35 mm. in breadth. The fully formed eggs are washed out of the bursa copulatrix when the female, flying over a pool, puddle or stream, dips the end of her abdomen into the fresh or stagnant water. Each egg is surrounded by a clear gelatinous material. The eggs hatch in 11 to 13 days. The length of the nymphal stage and number of instars are unknown. At maturity, the nymph measures about 24 mm. in length, and "may develop a very unkempt or frowsy appearance, the nondescript brown body then harboring colonies of long-stemmed protozoans (*Vorticella*), while diatoms and clusters of sewage-like bacteria will accumulate profusely among the hairs." (Williams, 1936:294.) The naiad may readily be distinguished from the four other dragonfly naiads in the islands because the lateral spines on the abdomen are shorter than on any other species. The food habits of neither the adult nor the naiad are well known, but Williams has seen the adults feeding upon *Tanytarsus* midges and the larvae feeding upon *Culex* wrigglers. I have often seen the adults catching a variety of unidentified Diptera along mountain trails or in deep, narrow gulches.

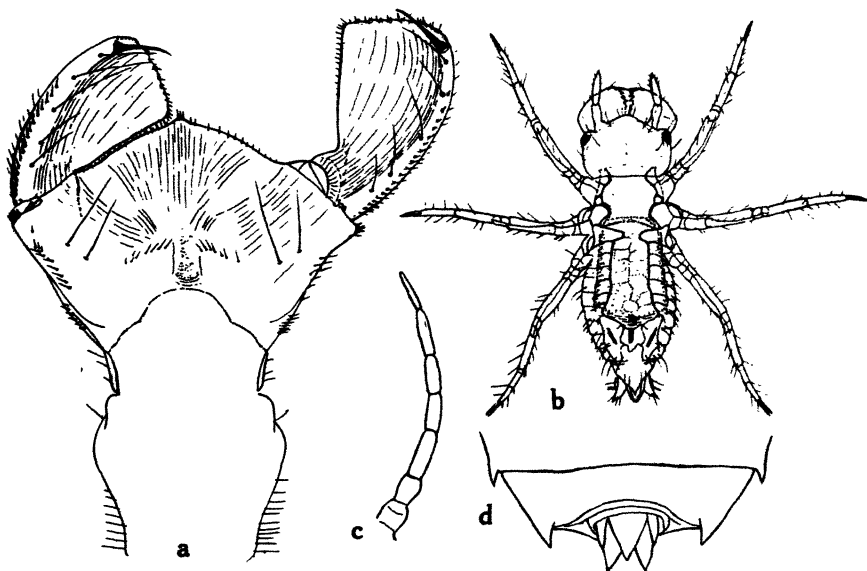


Figure 190—Details of the naiad of *Nesogonia blackburni* (McLachlan): a, inner view of labium of mature naiad; b, recently hatched naiad (tracheae and yolk mass showing); c, antenna of last-stage naiad; d, apex of abdomen of last-stage naiad. (From original drawings for Williams, 1936.)

In the box of this species in Perkins' personal collection now at the Bishop Museum there is the following note written by Dr. Perkins, which I include here for preservation: "15 unlabelled specimens (one broken) are from a gulch below Kalae, Molokai where there was a large congregation of this species, sunning themselves on dry stems a little before sundown. Many of the specimens I took were given away, and most (of the specimens seen) I did not attempt to catch. I never saw any other assemblage of this species elsewhere. R.C.L.P. II.1902." Some of Blackburn's material is also in Perkins' collection, and it bears the label "16" and "*Leptemis Blackburni*."

Genus **PANTALA** Hagen, 1861:141

This genus is represented in Hawaii by the most widely distributed dragonfly in the world. It is:

Pantala flavescens (Fabricius) (figs. 186, d; 187, e; 188).

Libellula flavescens Fabricius, 1798:285, type from India.

Pantala flavescens (Fabricius) Hagen, 1861:142.

Warren, 1913:72-82; 1915:7-36. Williams, 1936:295-298, figs. 4, 67, 68, bionomics.

The globe skimmer.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii.

Immigrant. Tropicopolitan. This species is widespread in the Pacific and is found on almost every island in Polynesia. The first Hawaiian record is that by McLachlan (1883:229), who recorded specimens taken by Mathew and Blackburn (and from Beechey's voyage?). There appear to be, however, no data to indicate when the species actually first became established in Hawaii. It has been seen several hundred miles at sea.

Warren (in both 1915 papers) and Williams (1936) have published accounts of this species. It is our most common and abundant dragonfly. Although it is predominantly a lowland insect, it may be seen often in the mountains, and occasionally up to about 8,000 feet. It begins its hunting early in the morning, and on warm evenings may fly after the sun has set. It occasionally comes to light in the evening. After a rain when the subterranean termite is swarming, groups of this skimmer will frequently fly back and forth through the clouds of emerging termites, eagerly devouring them as long as there is light enough for them to see their prey. They are abundant even in the city.

The whitish to yellowish eggs are deposited by the flying female as she dips her abdomen in almost any available water, from rain water puddles to fish ponds, reservoirs and rivers. Warren collected 816 eggs from one female. The incubation period is from five to seven days. There are 11 or 12 instars which, Warren found, take 55 to 101 days for completion according to the amount of food available. A specimen fed an abundance of mosquito larvae every four or five days molted only

three times. The larvae can fast for over two weeks without ill effects. The full-grown nymphs are about 25 mm. long.

Warren examined the intestinal contents of several hundred naiads and found over one-half of the food to consist of Diptera, mostly the larvae and pupae of *Chironomus hawaiiensis*. About one-fourth of the food was the ostracod crustacean *Cypris*. Protozoa, beetles, molluscs, ants, tadpoles, Odonata nymphs, Hemiptera, fish and worms, in that order, made up the remainder of the food taken. Other organisms eaten are shrimps, *Cyclops*, leeches, millepedes, *Nereis*, nematodes, rotifers and moths, and almost any insect that happens to fall into the water. Like other dragonfly larvae, these naiads are cannibalistic. An examination of 218 adults showed that Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, Corrodentia, Thysanoptera and spiders were eaten. Small Diptera lead the list of insects eaten (about three-eighths of all food taken), followed by small beetles, small bugs, small moths and Hymenoptera.

The following note by McLachlan (1874:92) is worthy of quotation:

Of *A. Junius*, *P. flavescens*, and *T. lacerata*, Mr. Mathew [who visited Hawaii aboard H.M.S. "Repulse" in June, 1873] says that they are abundant in the Islands, and prey on the produce of what the Hawaiians call the "army worm." It is a species of *Hadena*, and occurs in countless multitudes. These large Dragon-flies used (or seemed) to follow me in numbers as I walked through the grass, darting off to the right or left of me in full chase when I disturbed a moth. They were numerous on board our ship, although we were anchored more than two miles from the shore.

Genus **TRAMEA** Hagen, 1861:143

A single wanderer from North America represents this genus in Hawaii.

Tramea lacerata Hagen (figs. 186, b; 187, d; 188).

Tramea lacerata Hagen, 1861:145. Williams, 1936:298, figs. 66, 69, 70.

The raggedy skimmer.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii.

Immigrant. Described from North America. First recorded from Hawaii by McLachlan (1874:92, and 1883:229) from specimens collected by Mathew and Blackburn.

This species is found in the lowlands, usually sparingly, but occasionally in considerable numbers in certain localities. It is less common than *Pantala flavescens*, is difficult to capture and little is known of its life history in Hawaii. It lays its eggs in a manner similar to that practiced by *Pantala* and *Nesogonia*; that is, they are washed from the tip of the abdomen. The greenish yellow and brown naiads are about an inch long when full grown.

Blackburn's specimen of this species is a dermestid-eaten individual in Perkins' collection at the Bishop Museum. It has neither date nor locality labels.

The conspicuous color pattern alone will serve to distinguish this species from all the others in Hawaii.

Suborder ZYGOPTERA Selys-Longchamps, 1854

Damselflies (Hawaiian name: "pinao-ula")

Wings held folded vertically and close together over back in repose; both pairs closely similar in size and shape, narrowed or petiolated toward base; an extra branch of media (Ms) takes place of Rs found in the Anisoptera; bridge and oblique vein absent. Head transverse; eyes button-shaped, projecting laterally at sides of head, separated by a space greater than their dorsal diameter; median lobe of labium deeply cleft. Male with four anal appendages, two superior and two inferior, the inferiors not homologous with the inferior anal appendage of the Anisoptera; penis not distinctly jointed; female with superior appendages only; ovipositor developed. Larvae with three caudal gills exposed (cercobranchiate), one medio-dorsal, two latero-ventral; rectum also used for respiration but not fitted with true tracheal gills as in Anisoptera; gizzard with eight to 16 radially symmetrical folds. (Modified from Tillyard, 1917:273.)

This suborder contains one of the most interesting and remarkable of all the endemic groups of Hawaiian insects. *Megalagrion*, and it is the only aquatic group that is developed to any extent. Also, two immigrant forms—a species of *Enallagma* and one of *Ischnura*—are now well established here.

Damselflies are much less active and are smaller, more fragile insects than dragonflies. Some of our species have a feeble sort of flight and can be captured with the hands, whereas the dragonflies are swift, agile, wary creatures, often most difficult to capture.

Native Hawaiian damselflies were much commoner and more numerous before fresh-water fishes and frogs were introduced to the islands. They will probably become rarer with the passing of the years. Some of the native species were abundant in the city of Honolulu, and it is a pity that these delicate, beautiful creatures cannot maintain themselves against the introduced predators and changed environmental conditions.

Superfamily COENAGRIODEA Tillyard, 1926

Family COENAGRIIDAE Tillyard, 1926

This is the largest of the two families of Zygoptera, and it is cosmopolitan in distribution. There are no representatives of the Agriidae found in Hawaii. This family is distinguished from the Agriidae by the fact that it has only two instead of several ante-nodal cross-veins.

The use of Coenagriidae in place of Coenagrionidae follows Tillyard's (1926:80, footnote) explanation of the proper forms of these words:

It is unfortunate that the fine classical name *Calopteryx*, which was in general use unchallenged for three-quarters of a century, has to be discarded by the Law of Priority, the type of the Linnaean genus *Agriion* being the insect which had been known for all that time as *Calopteryx virgo* L. The new name required for the genus whose type had been known as *Agriion puella* L. was supplied by Kirby, viz *Coenagrion*, who also changed the family name to Coenagrionidae,

by analogy with the old form Agrionidae. The name *Agrion*, however, is derived from the Greek *agrios*, wild, neuter *agrion*, a wild thing, stem *agri-*, and hence the correct family names are Agriidae, Coenagriidae, Megapodagriidae, and the superfamily names Agrioidea and Coenagriidea.

Subfamily COENAGRIINAE Tillyard, 1926

KEY TO THE GENERA FOUND IN HAWAII

1. Fore wings with five or more, usually six or more, cross-veins between subnodus and the cross-vein which joins R_2 at or slightly distad of origin of R_3 (Occasionally specimens of *Enallagma* with five cross-veins are found, but they may be distinguished by their terminalia and general facies.) Figure 178 **Megalagrion** McLachlan.
Fore wings with only three or four such cross-veins in our species 2
2. Fore wings with three such cross-veins **Ischnura** Charpentier.
Fore wings with four such cross-veins **Enallagma** Charpentier.

Note: These character differences have been found convenient for use in separating the species of *Ischnura* and *Enallagma* found in Hawaii and are not intended for use in other localities.

Genus MEGALAGRION McLachlan

Megalagrion McLachlan, 1883:237. Genotype *M. blackburni*.

Hawaiiagrion Kennedy, 1920:86. Genotype *M. xanthomelas*.

Kilauagrion Kennedy, 1920:86. Genotype *M. nesiotes*.

Oahuagrion Kennedy, 1920:86. Genotype *M. oahuense*.

This genus is one of the most remarkable of all the Hawaiian Insecta. Its species are among the largest and most striking in the fauna. Only the dryest low-

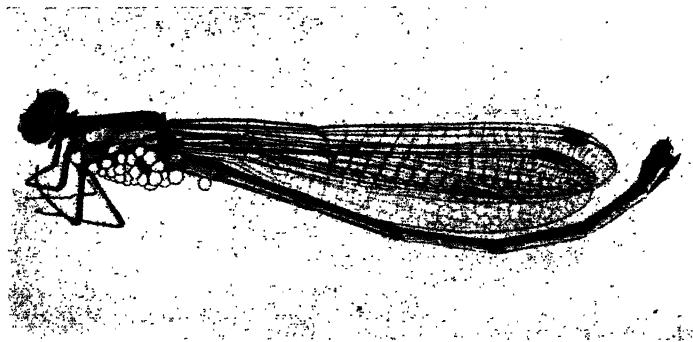


Figure 191—A female *Megalagrion* with the thorax and base of the abdomen infested with mites (Mountain View, Hawaii). (After Williams, 1936.)

lands and barren, extreme highlands are uninhabited by these net-winged creatures. Rivers and ponds have their representative species, as do wet banks and waterfalls; some species are arboreal, and at least one is truly terrestrial. The group was one of Perkins' favorites, and is one of the most extensively collected and probably the most completely known of all of the Hawaiian insects. Yet much remains to be studied and elucidated. No new species have been found since Perkins' explorations.

In this genus we find magnificently displayed the results of insular evolution and speciation. We have widespread, geographically variable species and remarkably isolated, highly specialized forms. A detailed study of the group will unfold to the student the marvels of evolution in a most dramatic way. For example, let us take *Megalagrion oahuense*. This is the most divergent of the group and is one of the most unusual of all Odonata. The nymphs of this species, unlike any other known form, have adapted themselves to a life on land. The naiads crawl about in search of their prey in the ground litter beneath dense clumps of fern. The larvae are morphologically modified for such a life. This species has taken a great step from the typical aquatic habit of the Odonata. Is it not true that this peculiar species shows us how a new order of insects could arise? Here before us we have the essence of evolution. Given time, is it not possible that this unusual damselfly whose nymphs now crawl about on damp ground could give rise to a new and distinct group of terrestrial carnivores? I believe so.

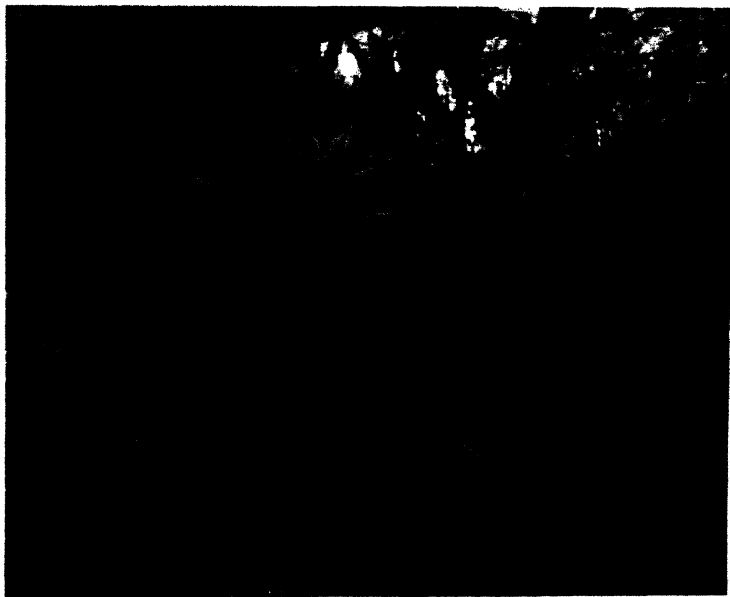


Figure 192—Mossy rain forest on Mount Kaala, Oahu, above 4,000 feet, showing some clumps of the liliaceous plant *Astelia veratroides* (in the middle) in the leaf bases of which the naiads of some of our native damselflies live. (After Williams, 1936.)

One of Perkins' earlier papers on the Hawaiian Insecta (1897:373) contains such an interesting account of the Odonata that I feel justified in quoting here his comments regarding the group.

Amongst the most important representatives of the Order of Neuroptera in the Hawaiian Islands, are the dragon-flies of the genus *Agrion*. Several species are found on all the more important islands of the group, and the range of many of them extends over several islands; wherein they differ from the greater part of the endemic insects, which are for the most part confined to a single island; or to one or two of those which lie most closely together. At the same time, when a series of examples of a species from different islands is compared, certain more or less constant differences are often observable, especially as regards size.

But the most interesting facts relate to the earlier stages or nymphs, which are aquatic and carnivorous. Excluding these dragon-flies and a few water-beetles, the insect fauna of the streams and pools is almost non-existent. The Ephemeridae, Perlidae, and Trichoptera, usually so numerous, are entirely unrepresented in the Islands, although the mountain streams, rising at high altitudes, with their superb waterfalls, and various temperatures, appear admirably adapted for many of these. It is therefore not a little surprising to find the group of dragon-flies so well represented, and that the individuals are so numerous, being on the whole the most conspicuous of all the endemic insects. In the absence of the groups above mentioned, I believe that their main food-supply comes from without, consisting of such creatures as accidentally fall into the water. Under ordinary circumstances this is not great, but after rain, when the streams rise very quickly, food becomes abundant. When the streams, as is often the case, become nearly dry, large numbers of creatures resort to the pools that are left, for the sake of the moisture, and the numbers that come to grief is often astonishing, the whole surface being covered with the drowned and drowning.



Figure 193—A view looking along the backbone of the Koolau Mountains southeast of Konahuanui, behind Honolulu, showing, in the foreground, a *Freycinetia* plant in the leaf axils of which some of our native damselfly nymphs live. (From Williams, 1936.)

There are, however, other species the nymphs of which live under very different circumstances. These have given up their aquatic life, and live hidden at the bases of the leaves of a liliaceous plant—*Astelia veratroides*. Sometimes a little water is held by the plant around the stem, but more often there is merely a collection of damp earth and dead leaves. These nymphs would even appear to dislike the collections of water, for in wet weather they often crawl halfway up the leaves, instead of remaining at the base, where the water accumulates. They differ in some points from those which frequent the water; they are shorter and stouter, and much more sluggish, and the caudal appendages are very short and thick, differing therein greatly from some of the aquatic species, the appendages of which form beautiful tracheal gills.

On the whole they are without doubt better off as regards a food supply than the aquatic species, for there is generally abundance of animal life around them. A number of interesting beetles breed only in this plant, and minute young of molluscs and earthworms are generally abundant in the same, as well as the larvae of small moths. Moreover nymphs of various sizes often frequent a single plant, and if hard pressed for food the larger, no doubt, devour the smaller individuals.

In consequence of these habits, some of these species of dragon-flies, although their powers of flight are feeble, may often be seen in numbers in localities remote from water, and where they would not naturally be looked for.

These terrestrial nymphs are able to endure extreme drought. On one occasion when out shooting, having no more convenient receptacle, I carried a number for the greater part of the day in an envelope. In the evening, although very dry, they were still quite lively. They were then placed in a tumbler of water, where they remained on the bottom, not being able to crawl up the sides. Here they remained for a day, apparently as happily as on dry land, when they were taken out and preserved.

To this account, the reader should not fail to add the excellent review of the group given by Williams (1936:300).

When McLachlan described *Megalagrion*, he said (1883:237), "I have established this division for the reception of two of the most magnificent species of the Légion *Aggrion* hitherto discovered." His main reason for erecting a new genus for *blackburni* and *oceanicum* was because some of the cells in the postcostal area were divided, thus making two rows of cellules.

Perkins did not adopt McLachlan's genus because, with his extensive collections and field observations, he was not only well aware of the great variability in wing venation but he was also familiar with the species in life. Perkins said (1913:clxxvi) that when an

extensive collection of Hawaiian species is examined, it is found that this duplication of cellules exists in all stages of development. Species that normally have a single post-costal row of cells sometimes have a number of these divided to form a double row. In some cases the post-costal area is simple on the wings of one side of the insect, partially double on the other. A similar phenomenon is also shown in the series of post-pterostigmatic cellules, where a similar complication of neuriation takes place, some species always having more or less a double row, others having sometimes a single and sometimes a partially double row, or the wings on either side may be different.

Megalagrion is supposedly a local development from an ancestral immigrant species belonging to the widespread Indo-Pacific genus *Pseudagrion*, which extends all the way to the Marquesas Islands. Kennedy (1929:978) said that *Megalagrion* "is so closely related to the oriental genus *Pseudagrion* that the more generalized

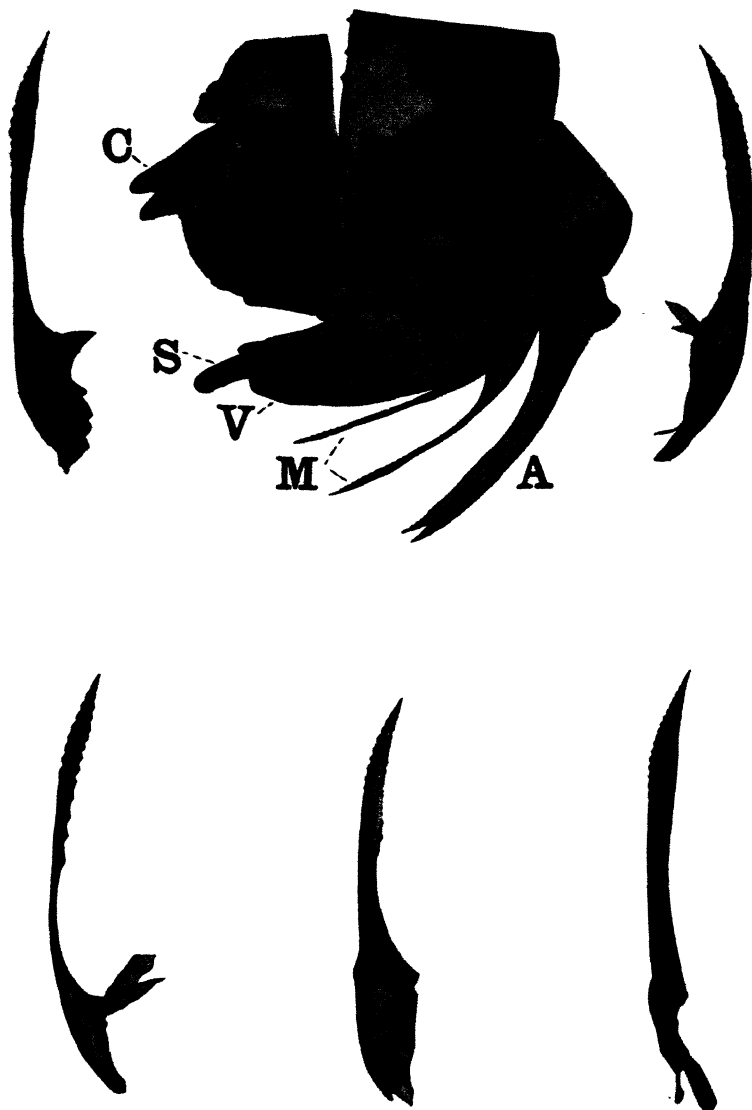


Figure 194—Ovipositors of some *Megalagrion*. Top, left, *M. hawaiiense* (McLachlan), median process; middle, *M. amaurodytum waianaeaeum* (Perkins), end of abdomen, somewhat compressed, showing components of terminalia: A, anterior processes; M, median processes; V, valve; S, style; C, superior anal appendages; right, *M. hawaiiense* (McLachlan), median process. Bottom, *M. koelense* (Blackburn), median process, left; *M. oceanicum* McLachlan, median process, middle; *M. oahuense* (Blackburn), median process, right. (After Williams, 1936.)

species of *Megalagrion* could be placed in *Pseudagrion* without hesitation, if found in the Orient." Perhaps *Megalagrion* is based as much or more on geographical isolation as it is on morphological grounds. It would be most worth while to make a detailed comparison of *Megalagrion* with various species groups of *Pseudagrion* from diverse localities.

The grouping of the species of *Megalagrion* has been unsatisfactory. Perhaps if complete keys had been made the relationships of the species would have been more clearly understood. The remarkable developments of the group may be misleading, and the species must be studied in the light of the special conditions obtaining in the Hawaiian Islands. The splitting of this group of interrelated species into several genera is, I believe, neither necessary nor justified. However, it cannot be denied that there are several distinct evolutionary lines represented. Perhaps if one studied only a few of the more distinct or divergent species, he would feel that, as Odonata go, he was examining representatives of distinct genera—but that is typical of oceanic faunas. However, a review of all the species presents a different picture. The removal of *nesiotes* to a distinct, monotypic genus, for example, is ignoring its several obviously close allies and serves only to confuse the picture. The separation of the large, mostly red-bodied species associated with *blackburni* into different groups conceals their true relationships.

Unfortunately, I cannot undertake a complete and detailed revision of this remarkable group here, because I have neither the time nor the experience necessary

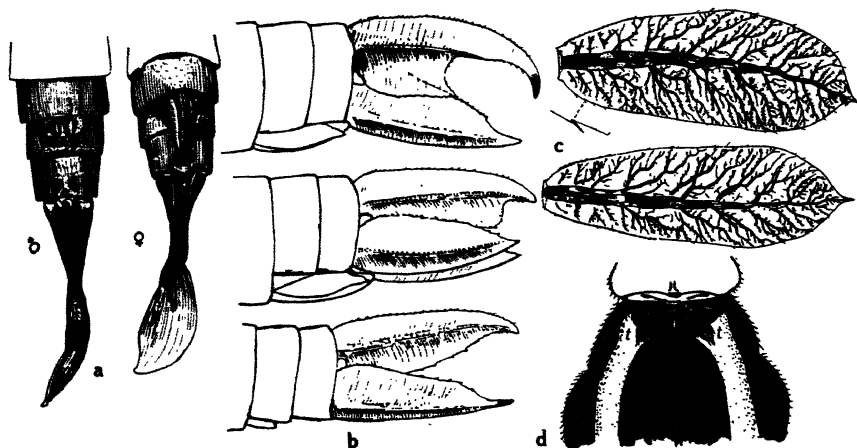


Figure 195—Details of some *Megalagrion*: a, extremities of nymphal exuviae of a male and female *M. xanthomelas* (Selys-Longchamps) to show characters differentiating the sexes in the naiaid stage; b, gills of the plant-inhabiting *M. koelense* (Blackburn) to show variation (the lower figure is probably from a penultimate stage naiaid); c, median and lateral gills of *M. xanthomelas* (Selys-Longchamps), a pool-inhabiting, strong-swimming form (compare these thin, densely tracheated gills with b); d, *M. oahuense* (Blackburn), dorsal view of part of thorax of a female to show the mesostigmal plate bearing tufts of hair at tt. (Rearranged from Williams' original drawings.)

for the task. However, a tentative grouping of the species as their relationships appear to me at this writing is suggested as a plan for future study by specialists. Largely on the basis of the male terminalia, I feel that the species may be divided into five major groups as follows:

Group I.—*blackburni*, *heterogamias*, *jugorum*, *molokaiense*, *oceanicum*.

Group II.—*eudytum*, *adytum*, *kauaiense*, *vagabundum*, *williamsoni*, *hawaiiense*, *nesiotes*.

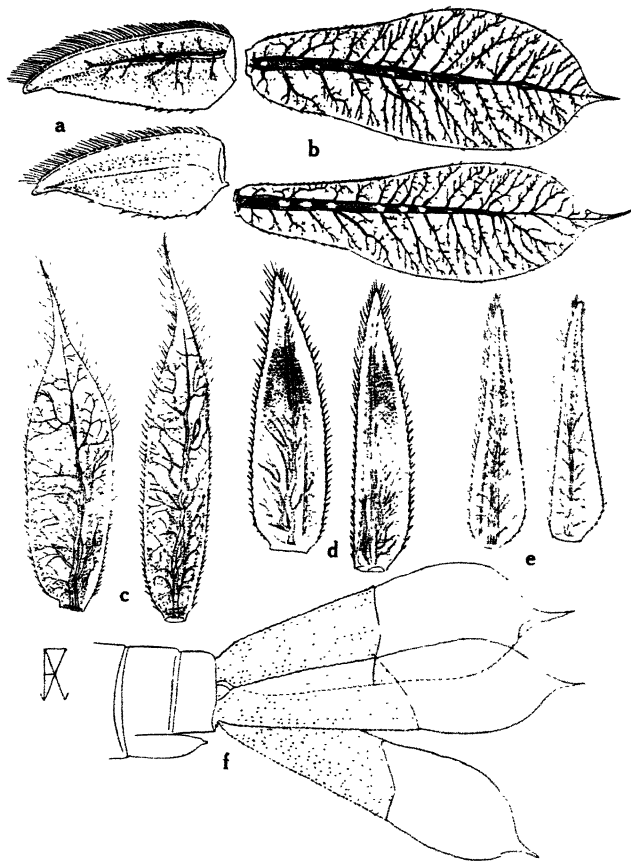


Figure 196—Gills of some *Megalagrion* species. Note the great difference between the gills of the non-swimming *M. amaurodytum waianaeaeum* (a) which lives at the bases of plant leaves and the actively swimming, stream-dwelling forms such as *nigrohamatum* (c). a, *M. amaurodytum waianaeaeum* (Perkins), median (bottom figure) and lateral caudal gills (upper figure); b, *M. leptodemas* (Perkins), median (top figure) and lateral caudal gills; c, *M. nigrohamatum nigrolineatum* (Perkins), median and lateral caudal gills; d, *M. oceanicum* McLachlan, median and lateral caudal gills; e, *M. hawaiiense* (McLachlan), median and lateral caudal gills; f, *M. leptodemas* (Perkins), lateral view of caudal gills—the stippled basal sections indicate a somewhat thicker and darker colored area. (From Williams' original figures, 1936.)

Group III.—*koclense*, *amaurodytum*, *xanthomelas*.

Group IV.—*nigrohamatum*, *calliphya*, *leptodemas*, *pacificum*, *oresitrophum*, *orobates*.

Group V.—*oahuense*.

This grouping does not necessarily indicate the relationships of each species within its group, nor are the groups here arranged in an order to indicate evolutionary trends. Certain of these groups might well be subdivided into two or more subgroups. The keys and figures will serve to characterize the groups.

The variation of features which have been used as specific or generic characters in some localities is great among the species of *Megalagrion*. The criteria used elsewhere to separate species cannot always be applied to the Hawaiian species. Many important characters are in a state of plasticity. The terminalia and genitalia are subject to a certain amount of variation. The wing venation is unstable and

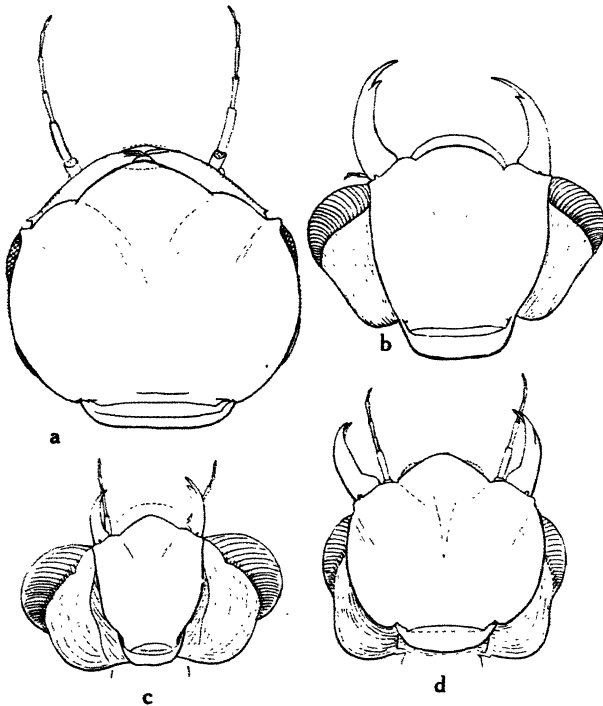


Figure 197—Undersides of heads of some *Megalagrion* nymphs: a, *M. nigrohamatum* (Blackburn)?; b, *M. amaurodytum waiianacatum* (Perkins), last stage; c, *M. hawaiiense* (McLachlan), last stage; d, *M. nigrohamatum nigrolineatum* (Perkins), last stage, from a different angle than a. (From the original drawings for Williams, 1936.)

highly variable. The wings on one side of a specimen may appear to belong to a different genus from those of the opposite side. The postocular spots may be present or absent, and the color of the body may be quite variable. Some of the species vary considerably in size. Also, there are locality (ecological) differences and island differences that add to the confusion.

Tillyard (1917:103) studied the gills of one of our *Megalagrion* (*koelense*) and found them so peculiar that he assigned a special category in his scheme of classification of gills to receive that species. He called the gills "The Reduced (Non-Functional) Type." He considered that in the gills of *M. koelense* (*asteliae*) "the tracheal system is so reduced that we may reasonably claim that they no longer function as tracheal gills." *M. koelense* is one of the species whose larvae live in the leaf axils of *Freycinetia* and *Astelia* plants. Tillyard said,

Viewed externally...the gills are striking in their shortness and stoutness; indeed, they do not, even at first sight, at all suggest true caudal gills, but rather a somewhat enlarged form of *anal pyramid* such as we find in the larvae of Anisoptera. In actual shape, as revealed by cross-sections, they might be classed as Triquetro-quadrate, or intermediate between this and the Saccoid Type. The median gill is broadly diamond-shaped in section, the laterals convexly triquetral. This shape is evidently brought about by the habit of resting the median gill upon the laterals, and the laterals upon the resting-surface. The larva is, to all intents and purposes, a ground-dweller, like those of the *Calopteryginae*; but the "ground," in this case, is not the river-bed, but the debris collected in the little leaf-pools. The return to the triquetro-quadrate *outward* form is, therefore, a very interesting example of the effect of change of habit on the form of the gills.

The gills of *Megalagrion* vary considerably among the several species according to habit and habitat. The terrestrial forms have the gills much reduced and thickened, the truly aquatic, actively swimming ones have large, delicate, leaf-like gills and those that crawl have smaller, more slender gills.

Some of the species are known to be attacked by a minute hymenopterous egg parasite, *Anagrus insularis* Dozier (1936:175). Occasionally adults are captured with aquatic mites attached to them (figure 191). It is thought that the mites are distributed from one area to another by attaching themselves to the imago when it emerges from its nymphal skin and by being subsequently carried away by the adult insect.

The naiads eat a variety of food, as the discussion elsewhere outlines. The adults feed on many kinds of insects, including Diptera, Lepidoptera, Hemiptera, Homoptera, Coleoptera, etc. They take not only flying insects, but may on occasion pick insects off vegetation or off the ground. The adults of most of the species emerge from their last pupal skin during the morning hours.

The fact that the life histories of about one-half of our species are unknown is a challenge to all keen observers.

There are recognized here 22 species with five possible varieties or races. Of these 22 species, 13, so far as is known, are restricted to single islands. The insular specific species, arranged with their islands, are as follows:

Kauai: *adytum*, *eudytum*, *heterogamias*, *kauaiense*, *orobates*, *oresitrophum*, *vagabundum*, *williamsoni*.

Oahu: *leptodemas*, *oahuense*, *oceanicum*.

Molokai: *molokaiense*.

Maui: *nesiotes*.

The species found on more than one island are as follows:

pacificum: Kauai, Oahu, Molokai, Lanai, Maui, Hawaii.

hawaiiense: Oahu, Molokai, Lanai, Maui, Hawaii.

nigrohamatum: Oahu, Molokai, Lanai, Maui, Hawaii.

amaurodytum: Oahu, Molokai, Maui, Hawaii.

calliphya: Molokai, Lanai, Maui, Hawaii.

koelense: Oahu, Lanai, Maui, Hawaii.

xanthomelas: Oahu, Molokai, Maui, Hawaii.

blackburni: Molokai, Lanai, Maui.

jugorum: Lanai, Maui.

This list will be subject to some revision when more extensive collections are made, especially on Molokai.

This distribution reflects not only the comparative ages of the islands (Kauai is the oldest) but also the isolation of the islands (Kauai is separated from Oahu, its nearest neighbor inhabited by the genus, by a distance considerably greater than the other inter-island channels). It is significant that Hawaii, the largest, but youngest, island of the archipelago, has no species restricted to it.

The following holotypes of *Megalagrion* are in the Bishop Museum: *calverti* (Perkins), male; *koelense* (Blackburn), male and female; *leptodemas* (Perkins), male and female; *nigrohamatum* (Blackburn), male; *nigrohamatum nigrolineatum* (Perkins), male; *oahuense* (Blackburn), male (this type is badly damaged); *satelles* (Blackburn), male; *tillyardi* (Perkins), male; *williamsoni* (Perkins), male.

The variation in the wing venation of the members of this genus is so great that any key based upon venation not only would be difficult to construct but probably would be misleading and inaccurate. One might find no great difficulty in separating many species on the basis of wing venation alone if only one or a few specimens of each species were examined; but the examination of series would break down the key characters. I have been unable to devote sufficient time to this study to enable me to present here a key including the females. Regrettably, then, a key based almost entirely upon the male terminalia follows. Because a number of the species are restricted to individual islands, I have, for the sake of convenience, divided the key into three principal sections based upon distribution.

KEY TO THE SPECIES OF MEGALAGRION—MALES

- A. Kauai species Section I.
- B. Oahu species Section II.
- C. Molokai, Lanai, Maui and Hawaii species Section III.

SECTION I.—KAUAI SPECIES

1. Superior appendages of male terminalia not reaching apices of inferior appendages 2
 Superior appendages of male terminalia extending beyond apices of inferiors 5
- 2(1). Superior appendages, viewed from side, conspicuously bifurcate; inferiors with a preapical dorsal tooth (Note: I have no definite record of this species from Kauai, but it is placed here in case it should be found on Kauai)..... *xanthomelas* (Selys-Longchamps).
 Superior appendages not bifurcate as viewed from side; inferiors not so armed 3
- 3(2). Superior appendages viewed from directly above, without a distinct tooth near base of inner edges..... *pacificum* (McLachlan).
 Superior appendages with a conspicuous tooth or spine on inner edges near base or with a small tooth and with apical margin of tenth tergite excised nearly to base 4
- 4(3). Tooth or spine on inner edge of superior appendages conspicuous, rising nearly to or to dorsum of appendage; tenth tergite emarginate only to about middle..... *oresitrophum* (Perkins).
 Spine on inner edge of superior appendage minute, not directed upward to dorsal level of appendage; tenth tergite excised nearly to base..... *orobates* (Perkins).

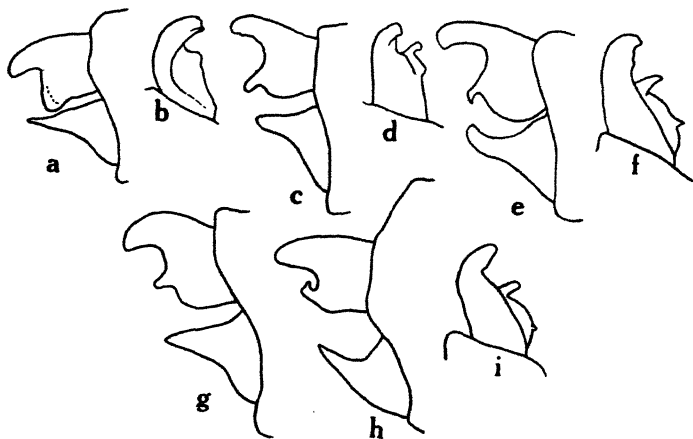


Figure 198—Details of some Kauai *Megalagrion* terminalia: a-b, *M. williamsoni* (Perkins), (a) lateral view, (b) left superior appendage from above and slightly oblique; c-d, *M. adytum* (Perkins), (c) lateral view; (d) left superior appendage from above and slightly oblique; e-f, *M. eudytum* (Perkins), (e) lateral view, (f) left superior appendage from above and slightly oblique; g-i, *M. kauaiense* (Perkins), (g) lateral view slightly oblique from beneath side, (h) as viewed directly at right angles from side, (i) left superior appendage from above and slightly oblique from right.

- 5(1). Superior appendages, as viewed from side, not bifurcate..... 6
 Superior appendages, as viewed from side, bifurcate (lower member usually in form of a large tooth)..... 7
- 6(5). Each superior appendage, as seen from above, with lower inner edge conspicuously folded, or rolled, inward and upward to form two conspicuous tooth-like processes (usually black-tipped, and dorsal part of appendage with an apical and subapical tooth-like angulation).....
**heterogamias** (Perkins).
 Superior appendages not so formed....**vagabundum** (Perkins).
- 7(5). Superior appendage, as viewed from above, with apical tooth on lower inner margin comparatively indistinct and rounded off, as in figure 198, a, b.....**williamsoni** (Perkins).
 Superior appendages with apical tooth on lower inner margin, as seen from above, strong and distinctly projecting, as in figure 198, i..... 8
- 8(7). Abdomen largely red; pterostigma usually crimson; terminalia as in figure 198, g-i.....**kauaiense** (Perkins).
 Abdomen not red, usually black; pterostigma not crimson; terminalia as in figure 198, c-d, e-f..... 9

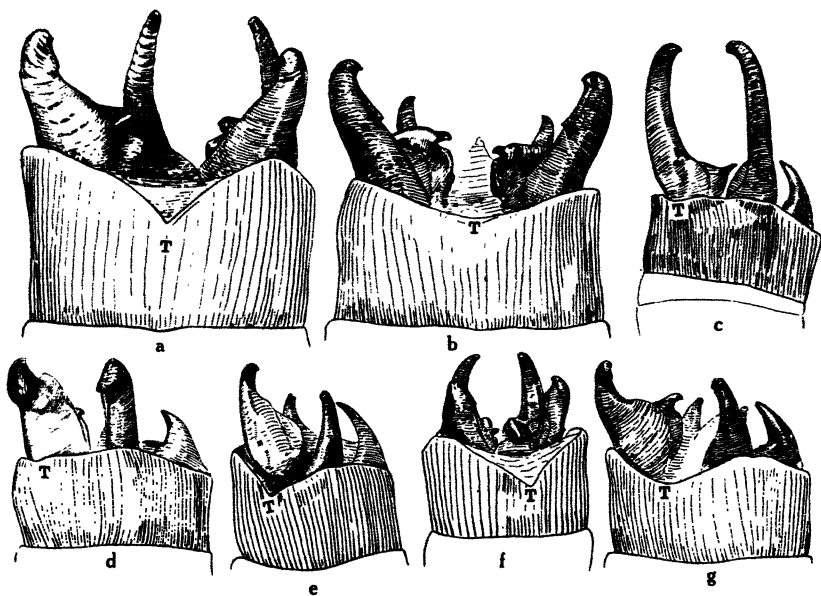


Figure 199—Male terminalia of some *Megalagrion*: a, *M. blackburni* McLachlan; b, *M. heterogamias* (Perkins); c, *M. nesiotis* (Perkins); d, *M. molokaiense* (Perkins); e, *M. vagabundum* (Perkins); f, *M. oresitrophum* (Perkins); g, *M. jugorum* (Perkins). "T" indicates the mid-point of the tergum. (Drawings made for this text by F. X. Williams.)

- 9(8). Head, thorax and first two abdominal segments conspicuously bluish white pruinose; terminalia as in figure 198, e-f, lower inner margin of superior appendage with anterior tooth small but discernible. **eudytum** (Perkins).
 Not pruinose; terminalia as in figure 198, c-d, lower inner margin of superior appendage without a small anterior tooth **adytum** (Perkins).

SECTION II.—OAHU SPECIES

1. Tenth tergite, viewed from side, conspicuously inclined upward and backward from base to apex; superior appendages of male terminalia turned outward, as in figure 201, f. **oahuense** (Blackburn).
 Tenth tergite and terminalia not so formed. 2
 2(1). Inferior appendages longer than superiors. 3
 Superior appendages as long as or distinctly longer than inferiors 5
 3(2). Superior appendages strongly bifurcate at apex; inferior appendage with a vertical tooth on dorsal margin just beyond middle. **xanthomelas** (Selys-Longchamps).
 Superior appendages not apically bifurcate; inferior appendage without such a tooth. 4
 4(3). Superior appendage usually touching or partially overlapping inferior; inferior bidentate at apex, figure 201, e.
 **nigrohamatum** (Blackburn).
 Superior appendage distant from inferior; inferior ending in a tapering point and not apically bidentate, figure 200, c **pacificum** (McLachlan).
 5(2). Superior appendages, as viewed from side, not or hardly extending beyond inferiors, about one-half to three-fourths as long as side of tenth abdominal segment, never as long or almost as long and not bifid at apex, as in figures 200, b; 201, a. 6
 Superior appendages, as viewed from side, almost or quite as long as side of tenth abdominal segment, and, or bifid at apex or not bifid, as in figures 200, b; 201, a. 7

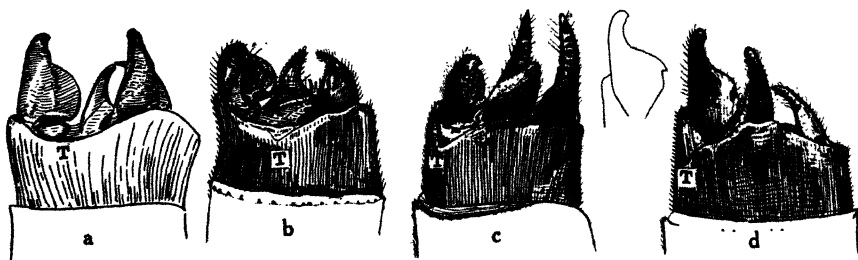


Figure 200—Male terminalia of some *Megalagrion*: a, *M. calliphya calliphya* (McLachlan); b, *M. leptodemas* (Perkins); c, *M. pacificum* (McLachlan); d, *M. hawaiiense* (McLachlan), with outline sketch of a clasper bearing a tooth. (a, drawn by F. X. Williams for this text; b-d, from original figures by Williams, 1936.)

- 6(5). Superior appendage, viewed from side very short, only about one-half as long as side of tenth abdominal segment, its height greater than its length, not attenuate, shaped as in figure 200, b; a small, slender-bodied species.....
 *leptodemas* (Perkins).
 Superior appendage, viewed from side, about three-fourths as long as side of tenth abdominal segment, its length greater than its height, attenuate, shaped as in figure 201, a; a large, heavy-bodied species.....
 *oceanicum* McLachlan.
 7(5). Superior appendages, viewed from directly above, each with a conspicuous, large, heavy, inwardly directed tooth on inferior margin, as in figure 201, b-c..... 8
 Superior appendages, viewed from directly above, not from side, without such teeth, as in figure 200, d (do not confuse projecting inferior appendages with teeth).....
 *hawaiiense* (McLachlan).
 8(7). Superior appendage, viewed from above, with tooth on lower margin nearer base than apex, as in figure 201, b.....
 *amaurodytum* (Perkins).
 Superior appendage, viewed from above, with tooth on lower margin nearer apex than base, as in figure 201, c.....
 *koelense* (Blackburn).

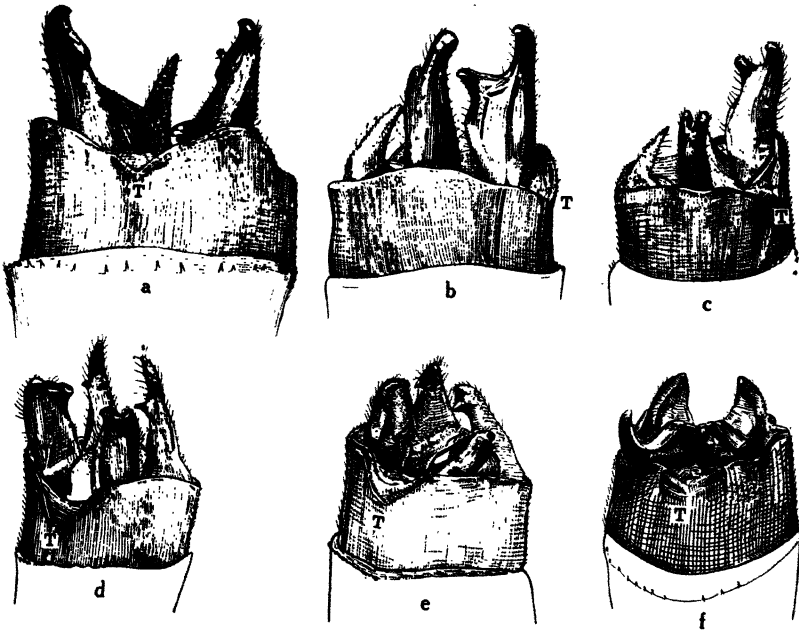


Figure 201—Male terminalia of *Megalagrion*: a, *M. oceanicum* McLachlan; b, *M. amaurodytum waianaeacum* (Perkins); c, *M. koelense* (Blackburn); d, *M. xanthomelas* (Selys-Longchamps); e, *M. nigrohamatum nigrohamatum* (Blackburn); f, *M. oahuense* (Blackburn). "T" marks the mid-point of the tergum. (From the original figures for Williams, 1936.)

SECTION III.—SPECIES FROM MOLOKAI, LANAI, MAUI OR HAWAII

1. Superior appendages of male terminalia, as viewed from side, not extending beyond apices of inferiors..... 2
 Superiors extending beyond apices of inferiors, usually conspicuously so 5
- 2(1). A very large, heavy-bodied, largely red-abdomened species (expanse across fore wings 60 to about 80 mm.); fore wings with about six cross-veins between media and cubitus between quadrilateral cell and cross-vein extending to subnode **blackburni** McLachlan.
 Small or medium-sized species whose fore wings have only two or three such cross-veins, less than 60 mm. in expanse across fore wings..... 3
- 3(2). Superior appendages strongly bifurcate at apex; inferior appendages each with a vertical tooth on dorsal margin just beyond middle..... **xanthomelas** (Selys-Longchamps).
 Superior appendages not apically bifurcate; inferior appendages without such a tooth..... 4
- 4(3). Each superior appendage distant from its inferior appendage; inferiors each ending in a tapering point and not apically bidentate (fig. 200, c)..... **pacificum** (McLachlan).
 Each superior appendage touching or partially overlapping its inferior; inferior bidentate at apex (fig. 201, e)..... **nigrohamatum** (Blackburn).
- 5(1). Superior appendages almost twice as long as length of tenth abdominal segment as seen from side (fig. 199, c)..... **nesiotes** (Perkins).
 Superior appendages shorter or hardly longer than side of tenth abdominal segment 6
- 6(5). Post-pterostigmatic cells at least in part subdivided by longitudinal connectives between cross-veins, as in figures 207, *jugorum*, and 208, *molokaiense*; pterostigma normally covering two cells; large, usually reddish-bodied species over 60 mm. in fore wing expanse and length of body over 50 mm. 7
 Post-pterostigmatic cells not so subdivided; pterostigma normally covering one cell; small or medium-sized species under 60 mm. in fore wing expanse and body usually less than 50 mm. long..... 8
- 7(6). Maui and Lanai species; male terminalia as in figure 199, g **jugorum** (Perkins).
 Molokai species; male terminalia as in figure 199, d..... **molokaiense** (Perkins).
- 8(6). Superior appendages, as viewed from directly above, with lower margin produced in a conspicuous and strongly developed, internally projecting, tooth-like process, thus making each appendage appear apically bifid when viewed from side or from beneath 9

- Superior appendages without such a process and not appearing apically bifid 10
- 9(8). Superior appendages, when viewed from above, each with tooth on lower margin nearer base than apex, as in figure 201, b.**amaurodytum** (Perkins).
 Superior appendages, viewed from above, each with tooth on lower margin nearer apex than base, as in figure 201, c **koelense** (Blackburn).
- 10(8). Superior appendage, as viewed from above, with a dorsally directed, tooth-like process, usually at least in part polished black, near base on inner face. **calliphya** (Perkins).
 Superior appendages without a trace of such a tooth-like process (as seen from above, not from side).....
 **hawaiiense** (McLachlan).

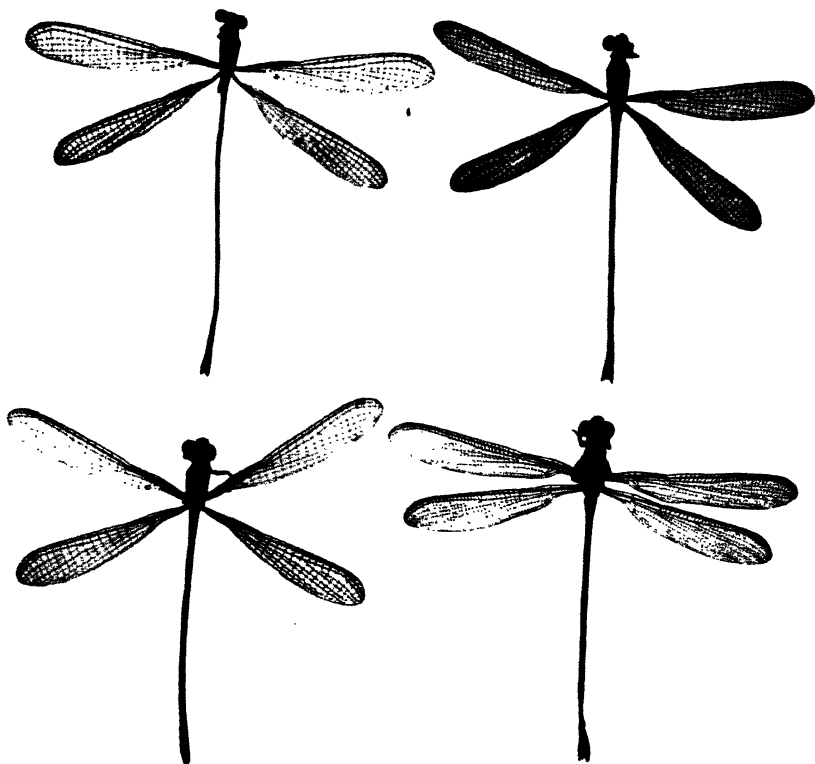


Figure 202—*Megalagrion*. Top: *M. adytum* (Perkins), left; *M. amaurodytum amaurodytum* (Perkins), right. Bottom: *M. amaurodytum peles* (Perkins), left; *M. blackburni* McLachlan, right. (Not to same scale.)

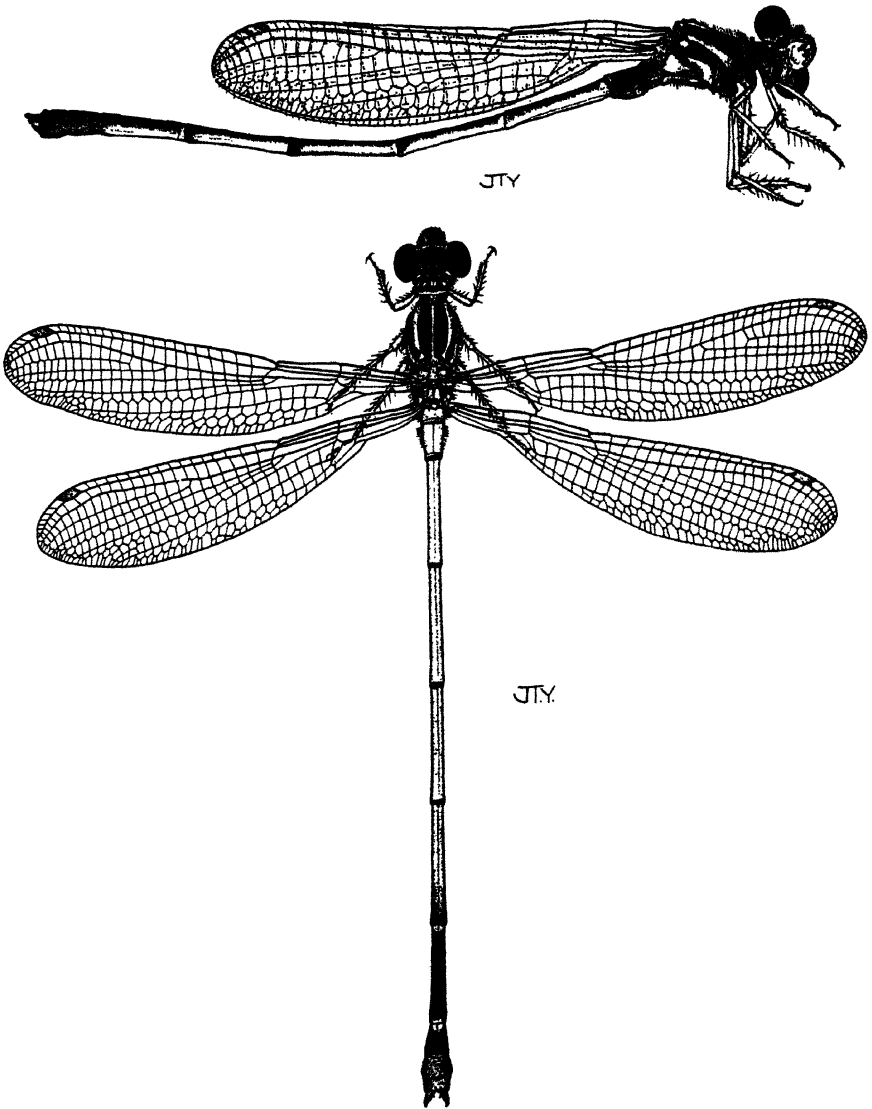


Figure 203—Top, *Megalagrion amaurodytum waianaeaeum* (Perkins), male, body length, 42 mm., from nymphal shell illustrated in fig. 211. Bottom, *M. oceanicum* McLachlan, male, wing expanse, 58 mm. (From Williams' original figures, 1936.)

Megalagrion adytum (Perkins) (figs. 198, c-d; 202).

Agrion adytum Perkins, 1899:69.

Agrion adytum variety *tillyardi* Perkins, 1910:695.

Megalagrion adytum (Perkins) Kennedy, 1917:11.

Endemic. Kauai (type locality: 4,000 feet; type locality of *tillyardi*: "near Lihue on a mountain stream.").

This species is allied to *eudytum* (Perkins); nothing is known regarding its habits.

The type of the "variety" *tillyardi* is in the Bishop Museum and has been labeled by Perkins as a synonym of *adytum*.

Megalagrion amaurodytum amaurodytum (Perkins) (fig. 202).

Agrion amaurodytum Perkins, 1899:66, pl. 5, figs. 7, 7a. (NOTE: These figures do not apply to *koelense* as stated in *Fauna Hawaiiensis*. See Perkins, 1912:180, for explanation.)

Megalagrion amaurodytum amaurodytum (Perkins) Kennedy, 1917:11.

Endemic. Molokai, Maui (no definite type locality cited by Perkins).

Williams (1936:332) found this form breeding in *Astelia* plants above 2,000 feet on Molokai. The mature nymphs attain a length of slightly more than 20 mm.

Perkins (1899:67) described, but did not name, a "Larger and darker var. from high ridges of W. Maui Mts. (4000 ft.)."

This species is closely allied to *koelense* (see discussion under that species). It is a variable species and "may be an entirely blackish insect, with much bluish white pruinosity on the head, thorax and the base of the abdomen, or it may be of a more metallic black with conspicuous thoracic pale markings, or in addition to much pale ornamentation the abdomen may be largely red." (Perkins, 1913: clxxvi.) Further studies of large series of specimens from many localities are essential before the status of the forms of this species can be properly understood.

Megalagrion amaurodytum fallax (Perkins).

Agrion amaurodytum variety *fallax* Perkins, 1899:67.

Endemic. Hawaii (no specific type locality given by Perkins).

Schmidt (1938:326) lists this as an aberration and a synonym of *M. amaurodytum peles*, but he gives no substantiating data. Perkins' original notes (1899:67-68) read,

Where the typical form abounds an extraordinary variety is sometimes found. This has the abdomen more or less red in both sexes, the third segment generally almost entirely so; the legs are almost wholly pale. The post-ocular spots are red or yellow, large and connected (or almost so) by a red or yellow line. The prothorax is much spotted and the longitudinal lateral lines of the dorsum of the thorax are broad and distinct, while the pale marks which border the eyes inwardly are connected by a transverse band just behind the posterior margin of the clypeus.

Megalagrion amaurodytum peles (Perkins) (fig. 202).

Agrion amaurodytum race *peles* Perkins, 1899:67.

Megalagrion amaurodytum race *peles* (Perkins) Kennedy, 1917:11, figs. 7, 8, penis.

Endemic. Hawaii (type locality not specified by Perkins, but between 2,000 and 4,000 feet in elevation, probably between Olaa and Kilauea).

Perkins refers to this as a dwarf form of the species; it has only three cellules between the quadrilateral and nodus.

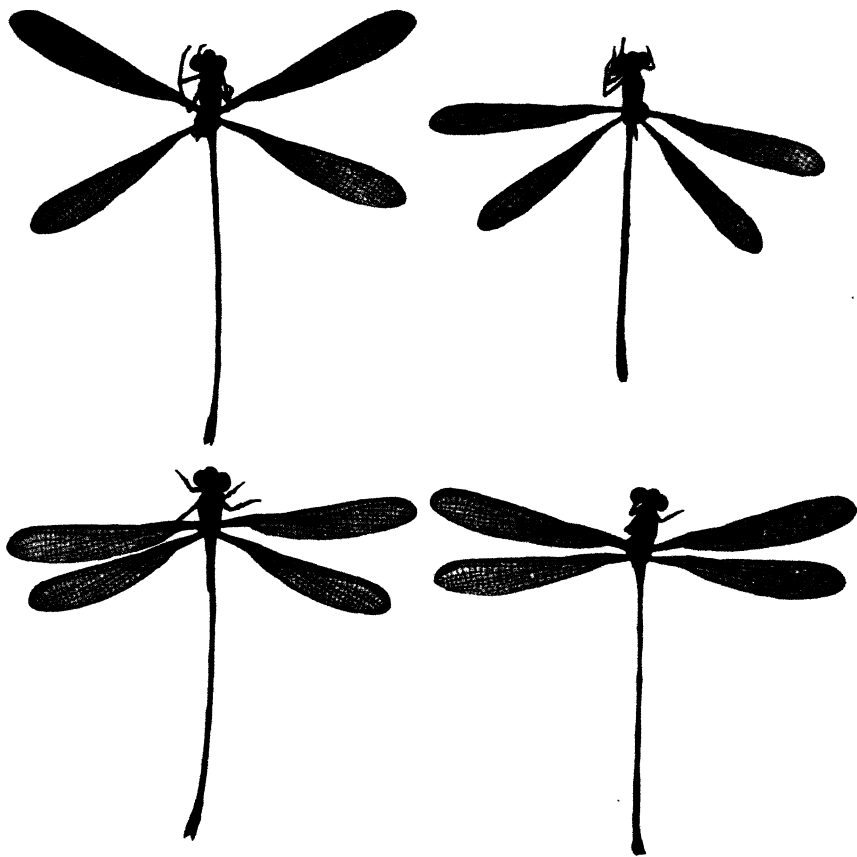


Figure 204—*Megalagrion*. Top: *M. calliphya calliphya* (McLachlan), left; *M. calliphya microdemas* (Perkins), right. Bottom: *M. eudytum* (Perkins), left; *M. hawaiiense* (McLachlan), right. (Not to same scale.)

Megalagrion amaurodytum waianaeaeum (Perkins) (figs. 194; 196, a; 197, b; 201, b; 203; 211).

Agrion amaurodytum race *Waianaeaeum* Perkins, 1899:67.

Megalagrion amaurodytum waianaceum, misspelling by Schmidt, 1938:326.

Williams, 1936:332, pl. 14, fig. 87, gills.

Endemic. Oahu (type locality: Waianae Mountains, 2,000 to 3,000 feet).

Williams (1936:332) has studied the larvae and habits of this form. The naiads live in the leaf axils of *Astelia* and *Freycinetia* on the higher peaks of the Waianae Mountains. The eggs are inserted in the leaf tissue (in the upper side of the midribs in *Freycinetia*). Their habit of living in the confined leaf axils, where the amount of available water is small, appears to have resulted in the loss of the ability to swim. Williams placed some nymphs in water and found that they were definitely ill at ease and unaccustomed to being submerged and appeared unable to swim. He says that the "mature nymph is in general brownish or slightly greenish brown; wood brown on the back and dark along the sides of the abdomen."

Megalagrion blackburni McLachlan (figs. 199, a; 202).

Megalagrion Blackburni McLachlan, 1883:238; 1892:178. Genotype.

Agrion blackburni (McLachlan) Perkins, 1899:76, pl. 5, figs. 15, 15a.

Kennedy, 1917:11, figs. 17, 18, penis.

Endemic. Molokai, Lanai, Maui (type locality: "At the head of Wailuku Valley"), Hawaii.

The nymphal stage of this species is included with that of *oceanicum* by Williams* in his key to the nymphs (1936:348); it lives in streams and on wet banks.

The only specimen in Blackburn's collection acquired by Perkins and now in the Bishop Museum was received by Perkins in fragmentary condition. It lacks head and abdomen, but the wings are intact.

This species belongs to the *heterogamias*, *oceanicum*, *jugorum*, *molokaiense* complex of large, heavy-bodied species.

Megalagrion calliphya calliphya (McLachlan) (figs. 200, a; 204).

Agrion (?) *calliphya* McLachlan, 1883:236.

Coenagrion Calliphya (McLachlan) Kirby, 1890:151.

Agrion calliphya McLachlan, Perkins, 1899:71, pl. 5, figs. 9, 9a; 1913:clxxxvii, figs. 3a, 3b.

Agrion ? *satelles* Blackburn, 1884:414, type from Haleakala, Maui, 4,000 feet.

Coenagrion ? *Satelles* (Blackburn) Kirby, 1890:151.

Agrion satelles Blackburn, Perkins, 1899:74.

Megalagrion calliphya calliphya (McLachlan) Kennedy, 1917:11, figs. 9, 10, penis.

Hawaiiagrion calliphya (McLachlan) Kennedy, 1920:86.

There is confusion regarding the synonymy involved here. Perkins (1899:74) said, "I cannot identify this species with any known to me. A large form of *Agrion deceptor* and a similar one of *A. calliphya* are common in the locality." The locality mentioned is Haleakala, Maui, 4,000 feet. Some years later, Perkins acquired Blackburn's collection; and two of Blackburn's examples of *satelles*, including the type, are now in Perkins' collection at the Bishop Museum. A note placed by Perkins with these examples reads, "Blackburn's type of *A. satelles*=*calliphya* McL. of F[auna] H[awaiiensis]." Also, on the specimen considered the type, Perkins attached the following note: "This is what I call *A. calliphya* in F. H." These notes would appear to indicate that *satelles* is a synonym of *calliphya*. However, the matter is not entirely clear to me, for Perkins wrote to F. X. Williams (letter of June 14, 1935) that "The status of *calliphya* McL. was somewhat uncertain, since, if I remember rightly, the specimen supposed to be this in Blackburn's coll. was not what I called *calliphya*, but what I considered a large form of *deceptor*. I was therefore very anxious that M. L.'s [McLachlan] type should be examined. It is quite likely that the specimen retained by Bl. may have been different from the one he sent McLachlan, since he (Blackburn) when he sent them to M. L. thought *deceptor* and *oceanicum* to be one species." Blackburn's example of what he called *calliphya* is in Perkins' collection at the Bishop Museum, and it bears the following label, written by Perkins: "*A. calliphya* sec. T. Blackburn. Really *A. deceptor*." As I understand it, Blackburn described *calliphya* as *satelles*, because he had incorrectly identified specimens of *deceptor* as *calliphya* and really compared his *satelles* with *deceptor*. In any case, Blackburn's type of *satelles* belongs to what is here called *calliphya* and not to *deceptor*.

- * Endemic. Molokai, Lanai (type locality: "about 2,000 feet"), Maui.
Nothing is known about the early stages of this form.

Megalagrion calliphya microdemas (Perkins) (fig. 204).

Agrion calliphya race *microdemas* Perkins, 1899:71; 1913:clxxvii, figs. 4a, 4b.

Megalagrion calliphya microdemas (Perkins) Kennedy, 1917:12, figs. 11, 12, penis.

Hawaiiagrion calliphya microdemas (Perkins) Kennedy, 1920:86.

Endemic. Hawaii (no definite type locality given by Perkins, but it is known to occur around Kilauea).

Nothing is known of the bionomics of this dwarf race.

Megalagrion eudytum (Perkins) (figs. 198, e-f; 204).

Agrion eudytum Perkins, 1899:68.

Megalagrion eudytum (Perkins) Kennedy, 1917:12, figs. 13, 14, penis.

Endemic. Kauai (type locality: "about 1,000 ft.).

This species is recorded in the *Fauna Hawaiiensis* from a single pair, but there

are seven additional specimens in Perkins' collection at the Bishop Museum which are labeled "Kauai, Lihue, 1000 ft." Nothing is known about its habits or early stages.

Megalagrion hawaiiense (McLachlan) (figs. 194; 196, e; 197, c; 200, d; 204; 205, a-r; 206).

Agrion (?) *hawaiiense* McLachlan, 1883:232.

Coenagrion Hawaiiense (McLachlan) Kirby, 1890:151.

Agrion hawaiiense McLachlan, Perkins, 1899:64.

Megalagrion hawaiiense (McLachlan) Kennedy, 1917:13, figs. 35-36, penis.

Agrion calverti Perkins, 1910:694 (type from near Honolulu, 1,200 feet, in Bishop Museum).

Agrion (?) *deceptor* McLachlan, 1883:235.

Coenagrion Deceptor (McLachlan) Kirby, 1890:151.

Agrion deceptor McLachlan, Perkins, 1899:74; 1913:clxxvii, fig. 2.

Megalagrion deceptor (McLachlan) Kennedy, 1917:13, figs. 15, 16 (not this species?).

Hawaiiagrion deceptor (McLachlan) Kennedy, 1920:86. New synonym.

Kennedy, 1917:12, figs. 15, 16, illustrates the penis of an atypical *deceptor*, or another species. See Calvert's footnote on page 13 of Kennedy's paper.

Endemic. Oahu (type locality: "at no elevation above the sea"). Molokai, Lanai, Maui, Hawaii. (Kennedy, 1929:980, records this species from Kauai, but his record may be in error. Perkins noted that it occurs on "All the Islands from Oahu to Hawaii inclusive.")

I believe that Williams (1936:324) was the first to publish the synonymy of *calverti*. He obtained the facts from Dr. Perkins, who wrote to him (June 14, 1935) as follows:

A. hawaiiense was for long a mystery to me. I did not get it at all in my earlier collecting. The first specimen I obtained must have been a stray one as it occurred on one of the high ridges I believe between Manoa and Pauoa and I never got another there. I described it as *Calverti*, n. sp. partly no doubt because Blackburn said that *hawaiiense* occurred at no great elevation above the sea and partly because I thought M. L.'s *hawaiiense* must have the appendages more different from those of *deceptor*, as he said nothing about their similarity. It was only later when I found *hawaiiense* in abundance on the Palolo stream and knew what a favorite collecting ground of Blackburn's this valley was, that I knew my *calverti* would be a synonym. Also I got hold of the sorry remnants of Blackburn's coll. which settled the matter. (these remnants were incorporated with my specimens now in Bishop Mus.) ... The limited distribution of *hawaiiense* seemed very curious, as if it were a very localized race of *deceptor*. ... Also at no great distance up Palolo, just above the point at which I used to leave the stream and go up a ridge (on the way to the crater) there was much *ieie*. Just before going up this, *hawaiiense* abounded in the stream bed around the pools—it was hardly flowing—and I found *Agrion* nymphs quite above the actual water in the moss growing on some of the rocks, as well as in the water. Some of these must have been *hawaiiense* as it and *nigrohamatum* were the only species round the pools at the time.

One of the principal characters used to separate *deceptor* from *hawaiiense* was the form of the superior appendage of the male terminalia. If there was a small tooth on the lower edge, the specimen was considered to be *deceptor*; if there was no tooth, the example was called *hawaiiense*. This is a highly variable and valueless character in this species. I have examined a series of males from various localities and have drawn a number of superior appendages to show how variable they are. *M. hawaiiense* is a variable species, and inasmuch as I have been unable to demonstrate specific differences between it and *deceptor*, I have reduced the latter to a synonym. The name *hawaiiense* has been used for the dark-bodied form from Oahu, and *deceptor* has been used for the usually red-bodied male form. Although the males of what has been called *deceptor* from Molokai, Lanai, Maui and Hawaii are normally largely red-bodied, melanistic males are common.

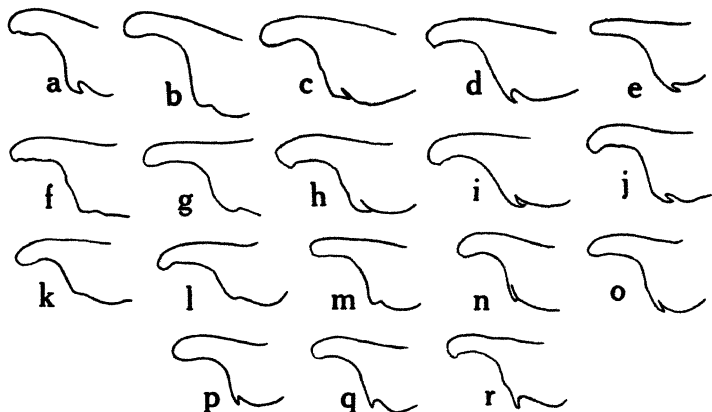


Figure 205—Sketches of lateral views of superior appendages of the male terminalia of various specimens of *Megalagrion hawaiiense* (McLachlan) to show the range of variation. a-e, Lateral views of superior appendages of examples from different localities: (a) Kilauea, Hawaii; (b) Haleakala, Maui, 8,000 feet; (c) Iao Valley, Maui; (d) Molokai; (e) Oahu. f-j, From a series of specimens taken at random from a set of males of the red form taken at the same time and place, Kula Pipe Line, Maui (Swezey, collector). k-r, From a random selection of eight specimens from a set taken by Perkins at the same time and place in Palolo Valley, Honolulu.

Williams (1936:324) said of the dark Oahu form (*hawaiiense*), "This is a damselfly of medium size that is largely metallic green in color, there being also some pale yellow on the thorax and very narrow bands of that color on the abdomen. It inhabits the canyons of both mountain ranges of Oahu, where I have found it at an elevation of less than 1,000 to nearly 4,000 ft. above the level of the sea."

Williams (1936:324-328, figs. 79, nymph; 86, gill; 116, male terminalia) made a detailed study of this species, and the following material is taken from his account. The eggs, which are about 0.8 mm. long, were found to be inserted in decaying or tender living plant material in very shallow water or on wet banks. The nymphs measure about 18 mm. in length when full-grown. They lead almost a terrestrial

life and live in the thinnest sheets of water on wet rocks or dripping banks. Williams calls them "rock creepers," and he occasionally found them crawling about completely out of the water. The nymphal food includes the larvae of the crane fly, *Limonia* (*Dicranomyia*) *grimshawi* (Alexander), oribatid mites, *Scatella* and other flies and their larvae, ants, Crustacea, etc. Williams found what he considers to be the nymphs of what was formerly called *deceptor* in a stream at 5,000 feet on Mauna Kea, Hawaii, and found that they fed mostly on *Tanytarsus* (Chironomidae).

Blackburn mistook what was later named *jugorum* by Perkins for this species (see note under *jugorum*), and he called this species *calliphya* (see note under *calliphya*). When Blackburn sent the male type to McLachlan, he thought that it was the same as what McLachlan described as *oceanicum*.

Megalagrion heterogamias (Perkins) (figs. 199, b; 207).

Agrion heterogamias Perkins, 1899:77, pl. 5, fig. 3.

Megalagrion heterogamias (Perkins) Kennedy, 1917:13, figs. 21, 22, penis.

Endemic. Kauai. Perkins did not give the exact locality of the type, but he mentioned (1899:77) that the species was widespread from about sea level to about 4,000 feet elevation.

This species is allied to *oceanicum*, *jugorum*, *molokaiense* and *blackburni*. Little is known about its early stages. Perkins (1913:clxxviii) found the nymphs "numerous amongst dead decaying leaves lying on the ground, and saturated with the wetness oozing from a perpendicular bank, at the foot of which they lay. There was no standing water, and the spot was at some distance from a river, and had no connection with this."

Megalagrion jugorum (Perkins) (figs. 199, g; 207).

Agrion jugorum Perkins, 1899:72, pl. 5, figs. 2, 11, 11a.

Megalagrion jugorum (Perkins) Kennedy, 1917:11.

Endemic. Lanai, Maui (type locality not specifically designated by Perkins).

Perkins stated that the species was found in the mountains of Lanai and the high ridges of West Maui at 4,000 feet, but nothing has since been recorded for this species.

Blackburn's example of this species is in Perkins' collection at the Bishop Museum. It was labeled *deceptor* by Blackburn, and has a label attached by Perkins which reads, "*A. deceptor* McL. sec. T.B.!! really *A. jugorum*."

This is a rare species belonging to the *blackburni* complex.

Megalagrion kauaiense (Perkins) (figs. 198, g-i; 207).

Agrion kauaiense Perkins, 1899:75; 1913:clxxvii, fig. 1a, 1b.

Megalagrion kauaiense (Perkins) Kennedy, 1917:11.

Endemic. Kauai (type locality not definitely stated with original description, but the species was recorded as having been widely distributed from 2,000 to 4,000 feet altitude).

This species, an ally of *williamsoni*, *eudytum* and *adytum*, is unknown in its immature stages.

Megalagrion koelense (Blackburn) (figs. 194; 195; 201, c; 207; 211).

Agrion ? *koelense* Blackburn, 1884:417.

Agrion koelense Blackburn, Perkins, 1899:65 (Note: pl. 5, figs. 7 and 7a do not apply to this species, but refer to *amaurodytum*. See Perkins, 1912:180, for explanation, and see note below).

Megalagrion koelense (Blackburn) Kennedy, 1917:13, figs. 27, 28, penis.

Agrion asteliae Perkins, 1899:66 (type locality: Oahu, 3,000 feet).

Megalagrion asteliae (Perkins) Kennedy, 1917:11, figs. 29, 30, penis. New synonym.

Tillyard (1917:103-106, figs. 30-32) discusses the gills of the nymphs of this species under the name of *asteliae*.

Endemic. Oahu, Lanai (type locality: a ravine near Koele), Maui, Hawaii.

This species is variable and confusing, the problems concerning it are involved and they cannot be answered in this work. However, I have synonymized *asteliae*, because I have been unable to find any constant characters to separate the two forms. An outline of some of the problems follows.

Perkins (1912:180) said, "Whether Blackburn's *A. koelense* is what I considered it is, or what I have called *A. amaurodytum*, I cannot tell with certainty till I examine his species. The members of the 'Koelense' group of Agrions, that superficially resemble one another, show much variability, the species are closely allied, and frequently occur mixed in the field, so they are not extraordinarily easy to distinguish." Blackburn's type material was later obtained by Perkins and is now in the Bishop Museum.

From the habits and gross features of the nymphs and adults, Williams was unable to differentiate between *asteliae* and *koelense*, and he notes (1936:333) that "*Megalagrion koelense* (Blkb.) and *M. asteliae* (Perk.) are very closely allied species best separated by the rather slight differences in the male claspers. They average a little smaller than *M. amaurodytum*. *M. asteliae*... on Oahu may fly with *M. koelense*."

Perkins (1899:66) said of *asteliae*, "A single pair taken in copula at Kilauea, Hawaii (4000 feet). The individuals from the two Islands [Oahu and Hawaii, i. e.] do not altogether agree, but I doubt whether they could be separated even with a long series of examples." When I first began this study, I noted that this distribution of *asteliae* inhabiting only Oahu and Hawaii, and *koelense* inhabiting Oahu, West Maui and Lanai, was very unusual. At that time I wondered if some error had not arisen as to locality or identification of the specimens of *asteliae* from Hawaii. I also considered the possibility that *asteliae* might be a form of *koelense*

and that the "species" was distributed from Oahu to Hawaii. However, the drawings of the penes given by Kennedy (1917:13, figs. 27-30) show what appear to be clear-cut differences which would nullify such an argument. The specimens of both *asteliae* and *koelense* used by Kennedy for his drawings came from the same place on Oahu (Mount Tantalus) and were collected by Perkins after the Odonata part of the *Fauna Hawaiënsis* was published. Perkins listed *koelense* only from Lanai and West Maui in his original report, but later (1906:50) noted that he found *koelense* very common on Mount Tantalus, Oahu.

In preparing the final part of this manuscript, I studied the penes of specimens from Perkins' collection and found that in both his series of *asteliae* and *koelense* there was obvious variation in the form of the penes. I have been unable to match exactly Kennedy's drawings. No two penes are completely alike. Kennedy's drawings appear in part to be diagrammatic, and one can be grossly misled by considering them representative of constant characters. I have come to the conclusion that it is not possible to separate *asteliae* from *koelense* by the characters of the penes—they are obviously variable. Moreover, the terminalia of the males upon which so much reliance is placed are also variable. Perkins (1912:181) gives a key to separate *amaurodytum*, *asteliae* and *koelense* based upon the form of the male terminalia.

The following information is of value and should be placed in the published record. In Perkins' material sent to the Bishop Museum is the specimen used for plate 5, figures 7, 7a, of his original *Fauna Hawaiënsis* report (1899), which illustrations I have noted above belong to *amaurodytum*. This example bears the label "*A. koelense*, near Koele, Lanai, 2000 feet, January 1894," and the following explanatory note written by Perkins: "This spec. was fig. in F. H. as *koelense* (V.7 and 7a) but is *amaurodytum*, not otherwise known from Lanai. I cannot help thinking that some mistake was made as to locality. The specimen was picked from the series of *koelense* for Wilson to figure because the terminal segments were separated and easy for him to handle, and no doubt was not specially examined by me before I gave it to him, as I had no suspicion that there was a wrongly named specimen in the Lanai series. Most likely one of the untrained boys in the Museum who labeled the insect made some mistake in labeling etc. The occurrence of *amaurodytum* on Lanai needs confirmation and the description pl. V. fig. 7 and 7a should read *amaurodytum* for *koelense*. R.C.L.P."

In a box of 49 specimens labeled *koelense* by Perkins is a note reading, "15 exx. on ridge above Palolo, settling on ieie vines, taken in cop. V-1912. Larvae numerous in the ieie leaves. R.C.L.P." ("Ieie" is the Hawaiian name for *Freycinetia*.) A note on one specimen reads, "This spec. was watched ovipositing in leaves of *Freycinetia*, not at base, but 1/3 from apex of the leaf." A female in Perkins' *asteliae* series bears the following label, "This was under *asteliae* in collection but looks to me casually more like *koelense*. 14-iv-29. R.C.L.P." It is evident that Dr. Perkins himself had difficulty in distinguishing these forms.

Dr. Williams (1936:333-339) has studied this species in detail in the field, and the following notes are based upon his observations. The pale-brown eggs,

which are about a millimeter long, are inserted in the midribs of the leaves of *Freyinetia* and/or *Astelia*. The females were observed to cling to the leaf above that in which the eggs were to be inserted, then extend the abdomen down to the leaf below and cut a slit in which the eggs were laid. Williams found that this species usually inserted a pair of eggs in each puncture, whereas the other species studied laid but a single egg in a puncture. The sites of oviposition are conspicuous in the leaves. The incubation period was found to be about three weeks. The nymphs are greenish brown to dark brown in color, and when full-grown measure about 18 mm. in length. They live in the axils of the leaves where water and trash collect, but they are able to withstand drying. The species now inhabits the mountains from about 1,000 feet upward. The nymphal food consists of many kinds of insects and other arthropods, including small wasps, bugs, carabid beetle larvae, various flies, damselfly nymphs, mites, spiders, isopods, amphipods, molluscs, etc. Perkins (1913:clxxix) said, "In wet weather, when a little water may collect at the bases of the leaves of the *Astelia* we have noticed that the nymphs will often be found to have crawled half-way up the leaf, as if they actually disliked the wet!"

This is one of the commoner species and can be found easily in the wet mountains where *Freyinetia* grows. It is peculiar that it has not been found on Molokai.

Megalagrion leptodemas (Perkins) (figs. 180, B; 196, b, f; 200, b; 206; 212).

Agrion leptodemas Perkins, 1899:70.

Megalagrion leptodemas (Perkins) Kennedy, 1917:12, figs. 5, 6, penis.

Williams, 1936:304, illustrated.

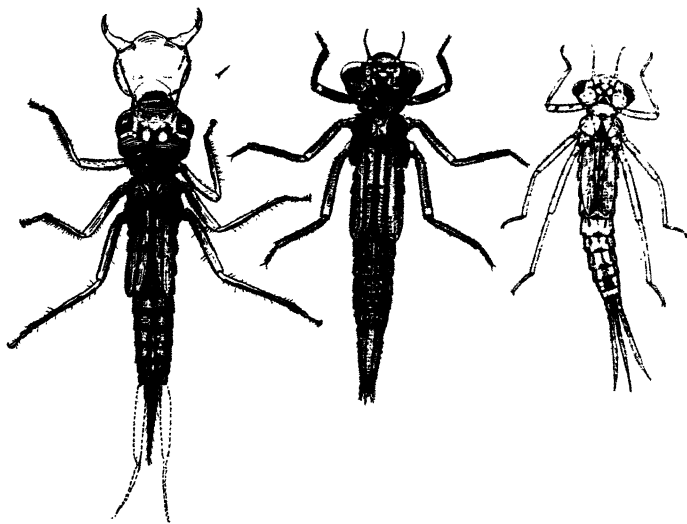


Figure 206—Naiads of *Megalagrion*: left, *M. nigrohamatum* (Blackburn), last stage, about 18 mm. long; middle, *M. hawaiiense* (McLachlan), last stage, 15.5 mm. long; right, *M. leptodemas* (Perkins), last stage, 14.2 mm. long. (From Williams' original drawings.)

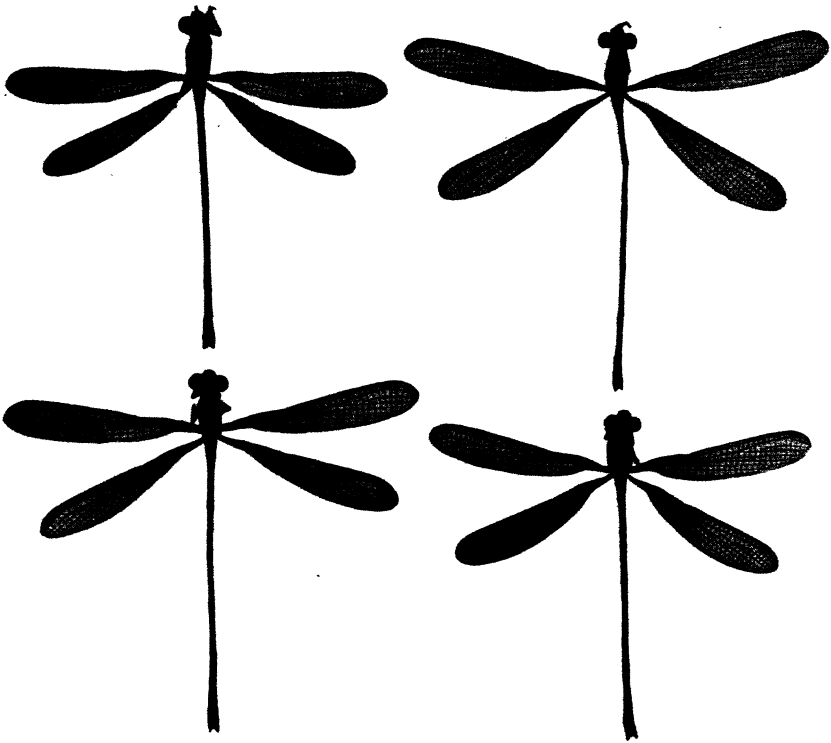


Figure 207—*Megalaagrion*. Top: *M. heterogamias* (Perkins), left; *M. jugorum* (Perkins), right. Bottom: *M. koclense* (Blackburn), left; *M. kauaiense* (Perkins), right. (Not to same scale.)

Endemic. Oahu (type locality: "Halemano," above 2,000 feet).

This species was described from a unique, but Perkins collected a series of specimens after the *Fauna Hawaiiensis* was published. Williams (1936:304–309) studied the species and has given us a good account of its habits. He says that "This is one of our smaller and more slender species. The male has a very red face—below the antennae—part of the thorax is red and the abdomen is red except for the intermediate portion. The female is more soberly colored; the abdomen while reddish at its extremity is for the most part blackish. It is sometimes abundant back of Honolulu. . . ." The life cycle of a reared example from egg to adult was four months. The eggs are inserted in plant tissue lying in water and may hatch in about two weeks. The nymphs are entirely aquatic, 17 to 18 mm. long when full-grown, and they have been well described by Williams. They live in mountain streams and stream pools where they feed largely upon dipterous larvae

such as *Culex* mosquitoes and chironomids, but other available arthropods are eaten. Williams notes that the nymphs closely resemble those of *M. xanthomelas*.

Megalagrion molokaiense (Perkins) (figs. 199, d; 208).

Agrion molokaiense Perkins, 1899:73.

Megalagrion molokaiense (Perkins) Kennedy, 1917:11.

Hawaiiagrion molokaiense (Perkins) Kennedy, 1920:86.

Endemic. Molokai (type from the east Molokai mountains about 4,000 feet).

The habits of this species are unknown. It is closely allied to *M. jugorum*, and I feel that further study may show that it is a local form of that species and hardly entitled to specific rank. It belongs to the *heterogamias*, *oceanicum*, *blackburni*, *jugorum* complex.

Megalagrion nesiotes (Perkins) (figs. 199, c; 212).

Agrion nesiotes Perkins, 1899:72, pl. 5, figs. 10, 10a.

Megalagrion nesiotes (Perkins) Kennedy, 1917:13, figs. 37, 38, penis; 1934:343, figs. 6-10.

Kilauagrion nesiotes (Perkins) Kennedy, 1920:86. Genotype of *Kilauagrion*.

Megalagrion dinesiotes Kennedy, 1934:343, figs. 1-5. New synonym. (In my reprint of Kennedy's paper, he wrote, "Later material intermediate between this and *nesiotes*, therefore probably a synonym.")

Endemic. Maui (type locality of *dinesiotes*). Hawaii (Perkins did not state where the holotype came from, and his type series was taken at a number of different localities on Hawaii).

The life history of this species is unknown.

Megalagrion nigrohamatum nigrohamatum (Blackburn) (figs. 197, a; 201, e; 206; 212).

Agrion ? nigro-hamatum Blackburn, 1884:415.

Coenagrion Nigrohamatum (Blackburn) Kirby, 1890:151.

Agrion nigro-hamatum Blackburn, Perkins, 1899:65, pl. 5, figs. 5, 5a.

Megalagrion nigrohamatum (Blackburn) Kennedy, 1917:13, figs. 31, 32, penis.

Hawaiiagrion nigrohamatum (Blackburn) Kennedy, 1920:86.

Williams, 1936:318-320.

Endemic. Oahu, Molokai, Maui (type locality), Hawaii.

This is one of the commoner native damselflies, and it is found from near sea level to a few thousand feet up the mountains. "The bright yellow face and the

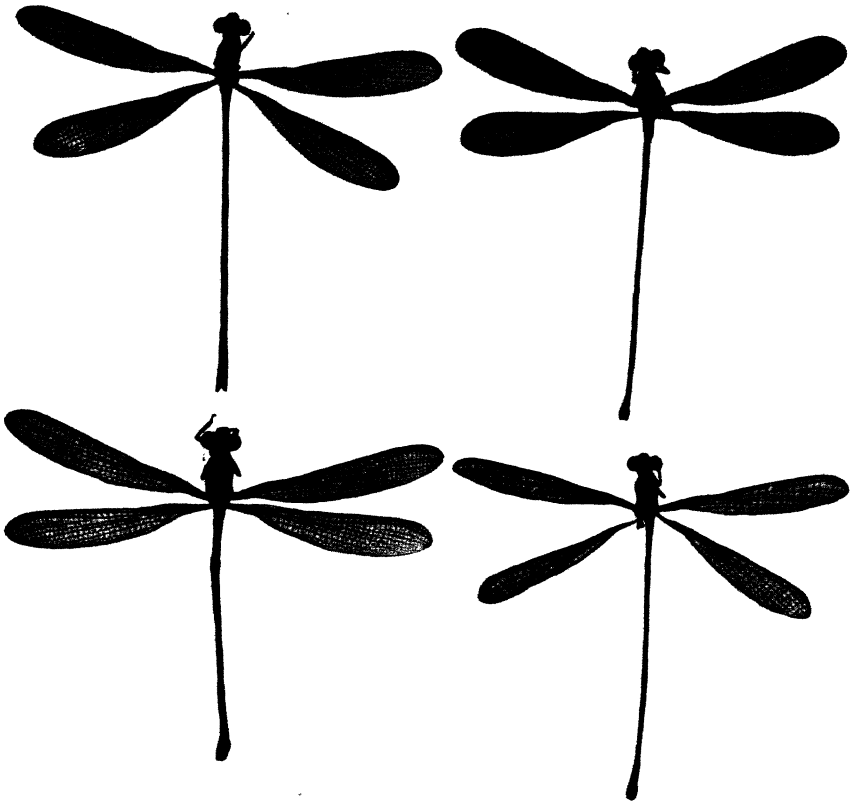


Figure 208—*Megalagrion*. Top: *M. molokaiense* (Perkins), left; *M. oahuense* (Blackburn), right. Bottom: *M. oceanicum* McLachlan, left; *M. orcsitrophum* (Perkins), right. (Not to same scale.)

colour of the eyes, which are bright green or turquoise blue on the lower half, and red on the upper, give this species a most remarkable appearance when flying around the streams. The colour of the eyes fades after death." (Perkins, 1899:65.) Williams (1936:318) states that "In the typical form *M. nigrohamatum* from Maui and Molokai, the knees of the legs are black, while in the race *nigrolineatum*, from Oahu and itself on the average a smaller insect, there is in addition, a black line along the upper side of the femora."

This is one of the species which breeds in streams and pools. The eggs are inserted in plant tissue in or near water. Unlike some of the other species whose larvae live exposed, these nymphs prefer to conceal themselves, for Williams found

the brown nymphs under stones and in masses of algae. The nymphs are described by Williams (1936:318), who found that they feed upon *Culex* and *Tanytarsus* larvae and other available material.

Megalagrion nigrohamatum variety **nigrolineatum** (Perkins) (figs. 196, c; 197, d; 212).

Agrion nigro-hamatum race *nigro-lineatum* Perkins, 1899:65.

Megalagrion nigrohamatum nigrolineatum (Perkins) Kennedy, 1917:13, figs. 33, 34, penis.

Hawaiigrion nigrohamatum nigrolineatum (Perkins) Kennedy, 1920:86.

Endemic. Oahu, Hawaii (Perkins did not designate a type locality).

The notes on the habits of the typical form apply to this variety. Perhaps if a long series of examples were examined from many localities it would be evident that the species is quite variable. Certainly the distribution is unnatural and reflects our incomplete knowledge of the form. I call it a variety instead of a race.

Megalagrion oahuense (Blackburn) (figs. 194; 195, d; 201, f; 208; 209; 210).

Agrion ? *oahuense* Blackburn, 1884:415.

Coenagrion Oahuense (Blackburn) Kirby, 1890:151.

Agrion oahuense (Blackburn) Perkins, 1899:74, pl. 5, figs. 12, 12a.

Megalagrion oahuense (Blackburn) Kennedy, 1917:13, figs. 25-26, penis.

Oahuagrion oahuense (Blackburn) Kennedy, 1920:86. Genotype of *Oahuagrion*. Williams, 1936:339-347, figs. 9, 10, 117, 123-128, bionomics.

Endemic. Oahu (exact type locality not recorded, but probably from the fore hills behind Honolulu).

To Dr. F. X. Williams great credit is due for his efforts and perseverance in making known the remarkable life history of this peculiar damselfly. Time and again he made arduous and diaphoretic field trips up the steep mountains of Oahu to track down and reveal the unique habits of this outstanding damselfly. I have been with Williams on some of his many trips, and I am entirely aware of the difficulties, time and labor involved during his research which cannot be appreciated fully by those unacquainted with the task. His long search was fruitful, and his outstanding contributions to Hawaiian entomology speak for themselves.

It "...is a rather large damselfly of very slender form.... The colors are somewhat dull, particularly in the female and consist chiefly of red, brown and pitchy black with some bronzy green on the thorax. Structurally, this species stands well apart from the others; the male is readily identified by his peculiarly shaped terminal claspers... the female by the tuft of tawny hair just behind each mesostigmal plate on the fore part of the mesothorax above..." (Williams, 1936: 339-340).

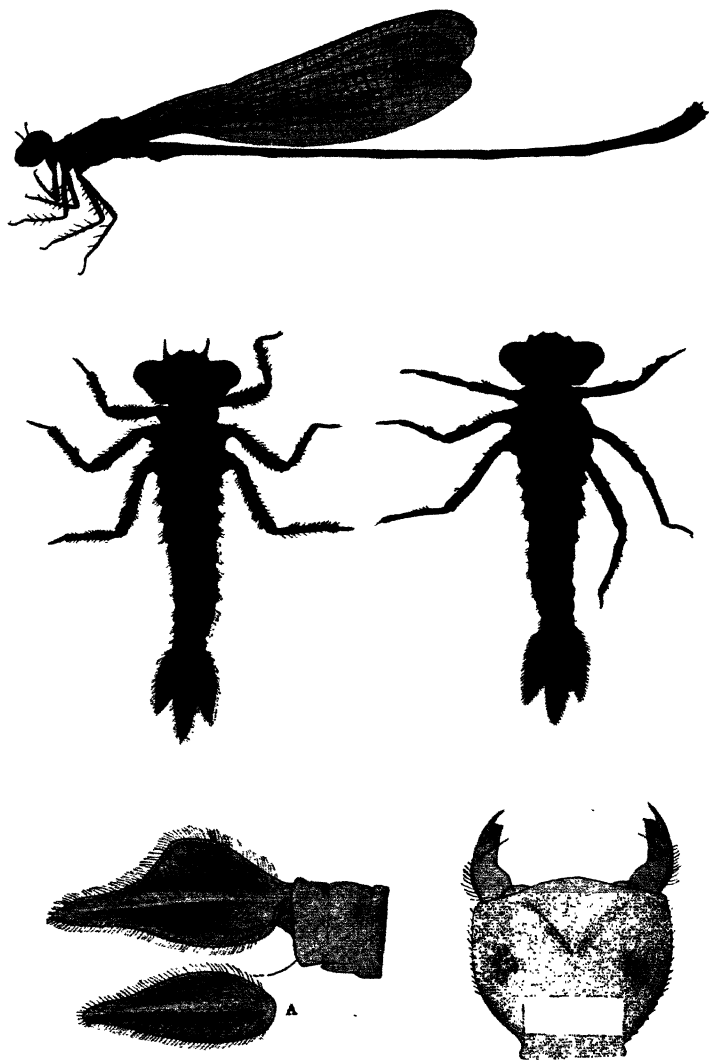


Figure 209—*Megalagrion oahuense* (Blackburn). Male at top. Middle: dorsal and ventral views of penultimate stage female naiad. Bottom, left: median and lateral gill (A) of above naiad; bottom, right: labium of above naiad from the inside to show two large setae on each side of the lateral lobes and two groups of small setae on the median lobe. (After Williams, 1936.)

In *Fauna Hawaiiensis*, Perkins (1899:74) gave the following notes: "High ridges of mountains of Oahu (3000 ft.). Nymphs living between the leaves of *Astelia veratroides*." Williams found that Perkins' assumption that the nymphs lived in *Astelia* plants was incorrect, and that the species has the most remarkable life history of any known member of the Odonata. Instead of being aquatic, this species is terrestrial! The eggs, which are pale orange and about 0.8 mm. long, are laid among the trash found under thickets of *Gleichenia linearis* fern. The nymphs, which inhabit the damp trash or leaf mold in the dense shade of the fern thickets, are the most hairy of the known Hawaiian nymphs. It appears that the development of the body hairs has to do with the retention of moisture on the nymphs' bodies. The gills are peculiarly formed, swollen and densely hairy. The length



Figure 210—A thicket of *Gleichenia linearis* fern growing on the slope of a ridge behind Honolulu showing where Dr. F. X. Williams found the remarkable terrestrial naiads of the native damselfly, *Megalagrion oahuense* (Blackburn). The fern is about three feet tall, and the foreground has been cleared in searching for the naiads. (After Williams, 1936.)

of the life cycle and the food of the nymphs have not yet been ascertained. The adults are on the wing throughout the year. They are usually low flyers and skim over the vegetation in search of such prey as midges. They also pick up insects, spiders and mites which are crawling on vegetation. The reader should consult Williams' classic discussion of his studies of this remarkable insect. The type of the species is now in the Bishop Museum. (See also my comments on page 343.)

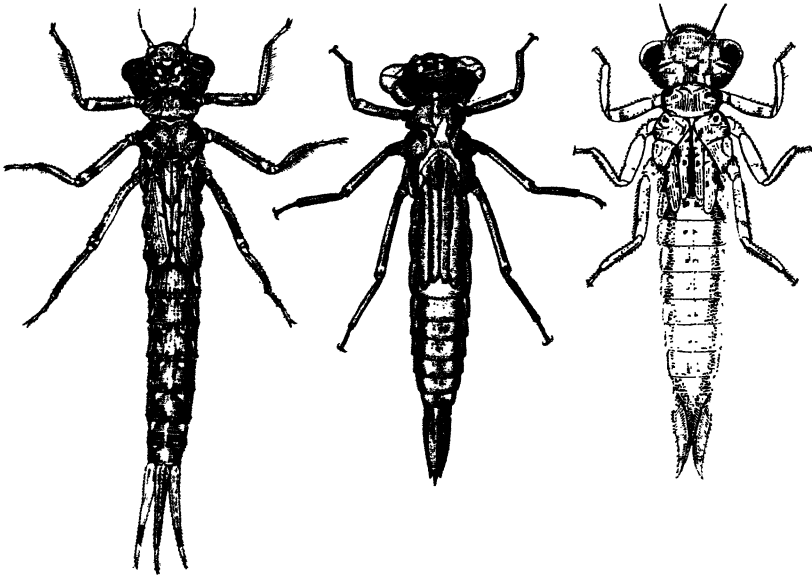


Figure 211—*Megalagrion* naiads: left, *M. oceanicum* McLachlan, last stage, 21.5 mm. long; middle, *M. amaurodytum waianaeae* (Perkins), cast skin from which the adult shown in figure 203 emerged, length 17.25 mm.; right, *M. koelense* (Blackburn), probably penultimate stage, 12.5 mm. long. (From the original figures for Williams, 1936.)

***Megalagrion oceanicum* McLachlan** (figs. 194; 196, d; 201, a; 203; 208; 211).

Megalagrion oceanicum McLachlan, 1883:239.

Agrion oceanicum (McLachlan) Perkins, 1899:76, pl. 5, figs. 14, 14a; describes female.

Kennedy, 1917:13, figs. 19, 20, penis. Williams, 1936:320–323, figs. 78, 88, 94, 95, 98, bionomics.

Endemic. Oahu (type locality: "at no great elevation above the sea").

This species, with *blackburni* and *heterogamias*, includes our largest and most conspicuous damselflies. The eggs of this species are inserted, often in great numbers, in the tissues—stems, leaves or roots—of several kinds of plants grow-

ing in or near water. The nymphs, which measure as much as 25 mm. in length when mature, are rather versatile in their habits. They have been found under stones and among roots and algae in running water; they swim well, but crawl up dripping wet banks, mossy rocks, and tiny waterfalls, and may leave the water and hunt about in moist places. They seem to prefer very shallow water and are better creepers or crawlers than swimmers. Their diet includes a variety of food among which Williams (1936:322) has found chironomid, ceratopogonid, tipulid and ephydrid fly larvae, caterpillars, Collembola, beetle larvae, adult flies, mites and earthworms. Williams found them to be easily reared in the laboratory. Perkins (1913:clxxviii) noted that the young nymphs were eaten by *Rhantus pacificus* (Coleoptera: Dytiscidae).

This elegant species belongs to a group whose bright-red abdomens are striking; it also has females which have black abdomens. In Perkins' box of this species

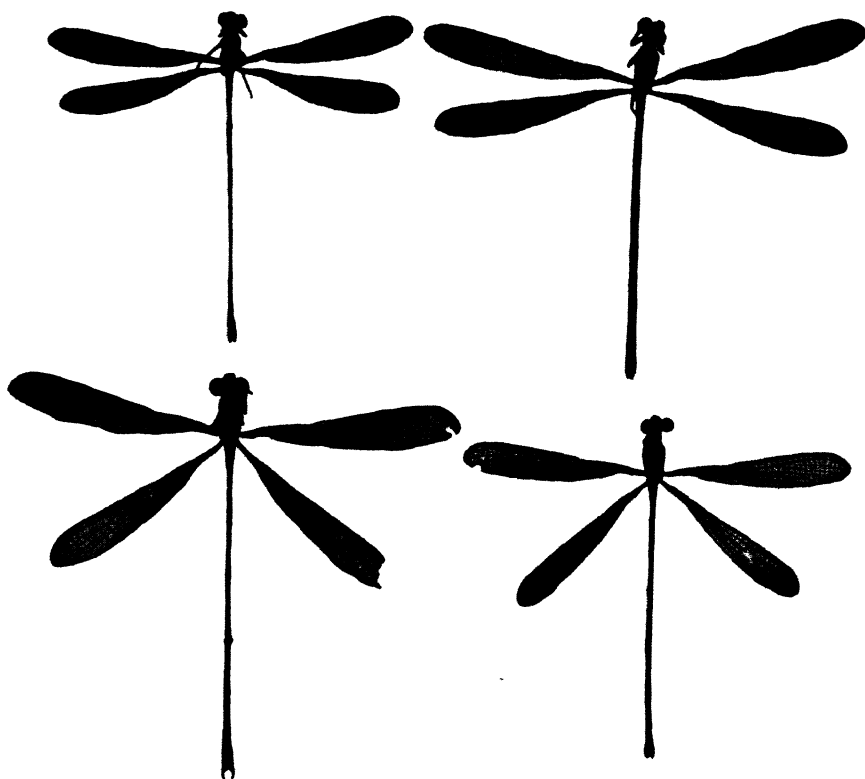


Figure 212—*Megalagrion*. Top: *M. leptodemas* (Perkins), left; *M. nigrohamatum nigrolineatum* (Perkins), right. Bottom: *M. nesiotes* (Perkins), left; *M. nigrohamatum nigrohamatum* (Blackburn), right. (Not to same scale.)

there is a note which reads, "The black bodied ♀ was not known to me when F. H. was written, as my specimens all came from W. side of Waianae Mts. where the ♀ ♀ were red-bodied. R.C.L.P." Also in Perkins' material is the specimen used by Wilson in preparing the illustrations of this species for *Fauna Hawaiiensis*.

Megalagrion oresitrophum (Perkins) (figs. 199, f; 208).

Agrion oresitrophum Perkins, 1899:69, pl. 5, figs. 8, 8a.

Megalagrion oresitrophum (Perkins) Kennedy, 1917:10.

Endemic. Kauai (type locality not designated other than in the mountains at 4,000 feet).

This species is closely allied to *leptodemas*, according to Perkins (1899:70). Nothing is known of its habits.

Megalagrion orobates (Perkins).

Agrion orobates Perkins, 1899:70.

Megalagrion orobates (Perkins) Kennedy, 1917:10.

Endemic. Kauai (type locality: above Waimea, 4,000 feet).

This species is said to be similar to *M. oresitrophum*. It was described from a single male specimen, and we do not have it represented in our named material at the Bishop Museum. Kennedy (1929:980) erroneously recorded the species from Oahu instead of Kauai.

Megalagrion pacificum (McLachlan) (figs. 200, c; 213).

Agrion (?) *pacificum* McLachlan, 1883:234.

Coenagrion Pacificum (McLachlan) Kirby, 1890:151.

Agrion pacificum McLachlan, Perkins, 1899:64, pl. 5, figs. 6, 6a.

Megalagrion pacificum (McLachlan) Kennedy, 1917:12, figs. 1, 2, penis.

Endemic. Kauai, Oahu, Molokai, Lanai, Maui, Hawaii (type material from Maui and Lanai at various elevations, not Lanai and Oahu as stated in original description; corrected by Blackburn, 1884:417).

Although this species is widespread and occurs at low elevations, its early stages have escaped general notice. In a letter to F. X. Williams, June 14, 1935, Dr. Perkins said "N.B. By an oversight on p. clxxviii F. H. line 24 '*hawaiiense*' should be *pacificum*, which is the stagnant water or pond species in so many localities. This and other errors I did not get a chance to correct in the final proof, when I was in Honolulu, as my returned corrections were too late!" Perkins' record (1913:clxxviii) on the early stages of this species reads, corrected, "*A. pacificum*, another small species, is more local than the preceding [*xanthomelas*], but also

seems to generally breed in stagnant water. When it frequents streams, like that of the Iao valley on Maui, we have noticed that its chief haunts are quiet small pools, often cut off, or at a distance, from the main stream. It also breeds numerously in upland ponds of considerable size, where these occur." Williams did not find the nymphs during his intensive research on the genus on Oahu.

Megalagrion vagabundum (Perkins) (figs. 199, e; 213).

Agrion vagabundum Perkins, 1899:75, pl. 5, figs. 13, 13a.

Megalagrion vagabundum (Perkins) Kennedy, 1917:13, figs. 23, 24, penis.

Endemic. Kauai (type series from 1,000- to 4,000-foot elevation, but no holotype locality given by Perkins).

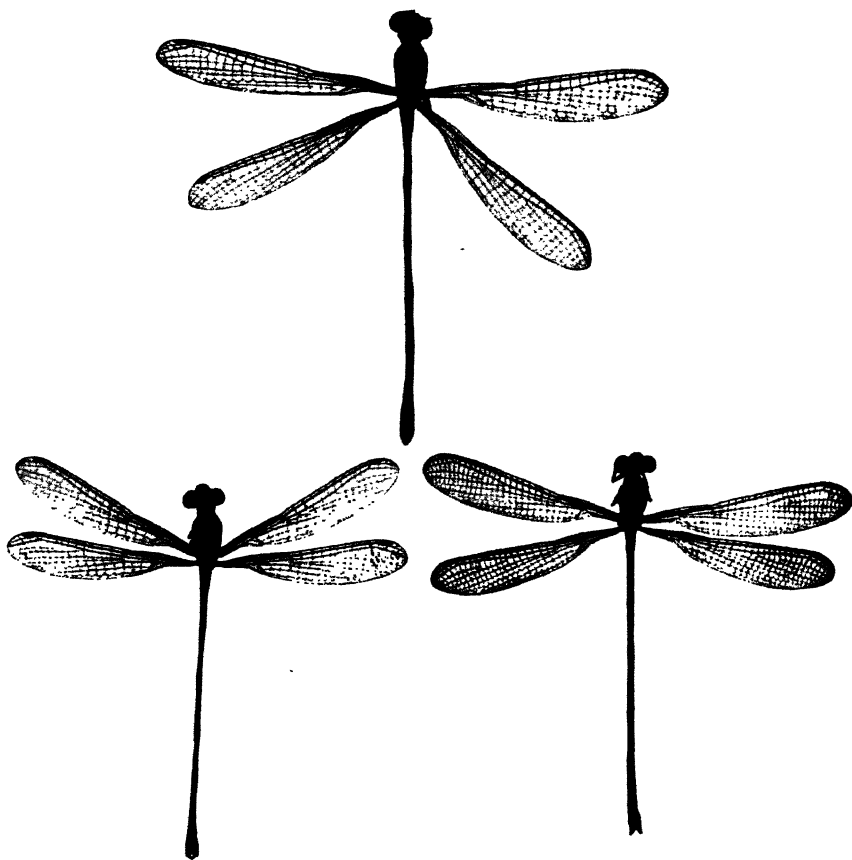


Figure 213—*Megalagrion*. *M. pacificum* (McLachlan), top; *M. xanthomelas* (Selys-Longchamps), bottom left; *M. vagabundum* (Perkins), bottom right.

Perkins found this species widespread in the mountains of Kauai. The life history is unknown. It is closely allied to *kauaiense* and appears to form a connecting link between *kauaiense* and *hawaiiense*. Judging from the male terminalia, *vagabundum* appears to be a *kauaiense* which has lost the apical tooth on the lower inner margin of the superior appendages.

Megalagrion williamsoni (Perkins) (fig. 198, a-b).

Agrion williamsoni Perkins, 1910:696.

Megalagrion williamsoni (Perkins) Kennedy, 1917:10.

Endemic. Kauai (type locality: "near Lihue on a mountain stream").

The unique male holotype of this species is in the Bishop Museum. Nothing is known regarding the habits of this species, which belongs to the *kauaiense* group.

Megalagrion xanthomelas (Selys-Longchamps) (figs. 180, C; 195, a, c; 201, d; 213).

Agrion (?) *xanthomelas* Selys-Longchamps, 1876:174. McLachlan, 1883:232.

Coenagrion (?) *Xanthomelas* (Selys-Longchamps) Kirby, 1890:150.

Megalagrion xanthomelas (Selys-Longchamps) Kennedy, 1917:12, figs. 3, 4, penis.

Hawaiiagrion xanthomelas (Selys-Longchamps) Kennedy, 1920:86. Genotype of *Hawaiiagrion*.

Williams, 1936:310-316, figs. 76, 89-91, 93, 104, bionomics.

Endemic. Oahu, Molokai, Maui, Hawaii (type from "Iles Sandwich").

I have been unable to find any definite records of this species being found on Kauai, or Lanai, but Kennedy records it from both islands. Perhaps he followed Perkins' statement (1899:64) that the species "Probably occurs all over the islands." It may occur on Lanai and Kauai, but I have seen no specimens or authentic records from those islands.

Perkins (1913:clxxviii) said that this "is a common insect in Honolulu gardens and in lowland districts generally, not usually partial to the mountains, though in the Kona district of Hawaii it is common about stagnant pools up to an elevation of about 3000 feet. It is very numerous in individuals under conditions totally changed from the natural; perhaps it now finds more numerous breeding places, and a more abundant prey in the numerous insects that have been introduced by man in the region it frequents." The introduction of *Gambusia* top minnows ("mosquito fish") has changed the lowland situation considerably in recent years, however, and the species is much less abundant than formerly.

The eggs, which are almost a millimeter long and amber in color, are inserted singly in punctures in such plants as *Commelina nudiflora* and *Marsilea villosa* near or beneath the surface of the water. The nymphs, which vary in color from greenish to dark brown and black are about 18 mm. long when full-grown, are entirely aquatic and are good swimmers. Their food consists principally of various aquatic dipterous larvae and the usual food materials available in ponds.

This was the first of the Hawaiian damselflies to be described. The type material was collected by G. F. Mathew, R.N.

Genus *ISCHNURA* Charpentier, 1840

This is a cosmopolitan genus of small damselflies known as "fork-tails" (this from the nymphs). Although the genus reaches its greatest development in the south and west Pacific, we have had no representative of the genus in Hawaii until recently when an immigrant became established. The structure of the wings, as mentioned in the key, and the form of the male terminalia readily serve to separate this genus from the two other genera of damselflies found in Hawaii.

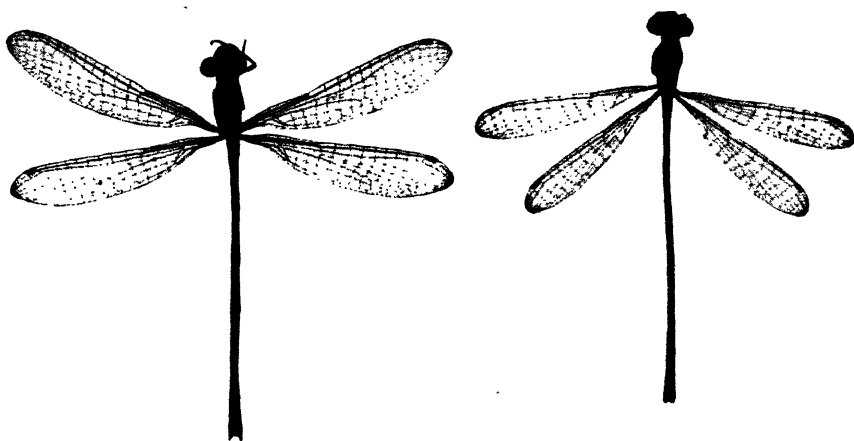


Figure 214—*Enallagma civile* (Hagen), male, left; *Ischnura posita* (Hagen), male, right.

Ischnura posita (Hagen) (figs. 214; 215, b-d).

Agrion positum Hagen, 1861:77.

Garman, 1917, gives good figures.

Oahu.

Immigrant. A common and widespread North American species. First found by Hoyt breeding in a lily pond in Honolulu in 1936.

Byers (in Needham and Heywood, 1929:350) gives a description of this species together with a figure of the male terminalia and a table of the nymphal characters. The nymphs, which measure about 17 mm. over-all when full-grown, can be separated from the nymphs of *Enallagma*, which they closely resemble, because they have long, slender, tapering gills (see fig. 215, b-d) instead of blunt ones. The nymphs I have seen have been a delicate green in color. The abdomen of both sexes in the adult has the tergites black with yellow basal bands on segments three to seven and blue on the apices of segments eight and nine.

The eggs are inserted singly in plant tissues and the species breeds in ponds. No detailed investigation of the life history and habits of this species has been made in Hawaii, but Williams has reared it from eggs laid in *Pistia* plants (*Proc. Hawaiian Ent. Soc.* 12[2]:221, 1945).

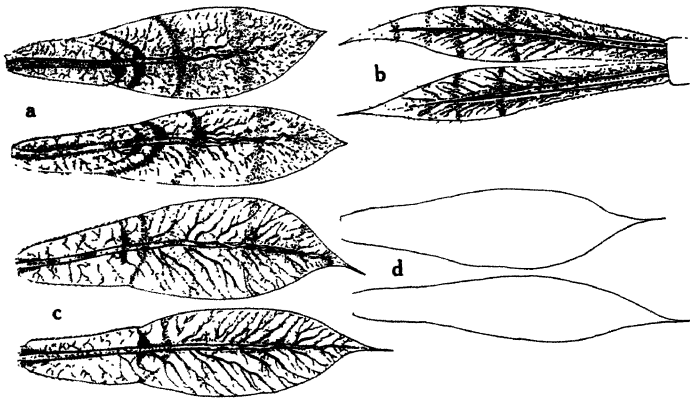


Figure 215—Caudal gills of our immigrant damselfly naiads: a, median and lateral gills of last stage naiad of *Enallagma civile* (Hagen); b, the same of a penultimate stage male naiad of *Ischnura posita* (Hagen); c, the same of a last stage female naiad; d, the same of a last stage male naiad (color pattern omitted, but similar to c). (Drawn for this text by F. X. Williams.)

Genus **ENALLAGMA** Charpentier, 1840

This is a widespread genus which is best developed in North America. The species have been called "bluets." One immigrant species from North America represents the genus in Hawaii.

Enallagma civile (Hagen) (figs. 180, D; 214; 215, a).

Agrion civile Hagen, 1861:88.

Garman, 1917, gives good figures.

Oahu, Molokai, Maui, Lanai.

Immigrant. First found by Williams in July, 1936, at Honolulu.

Byers (in Needham and Heywood, 1929:336) discusses this species, figures the male terminalia and gives characters of the nymphs. It may be distinguished easily from all our other damselflies because of its well-marked black and beautiful blue color pattern. The blue color generally fades to yellowish or brownish after death, however. Although *Ischnura posita* also has a black and blue color pattern, that species has the abdominal segments largely black above instead of mostly blue in the male. The females of this species have the dorsum of each abdominal segment black, however. No studies of its habits in Hawaii have yet been made. Its eggs are inserted in plant tissues beneath the surface of the water. I found adults of the species common on the summit of Mount Konahuanui, Oahu, above 3,000 feet, in May, 1943. They had been probably blown up to the mountain heights from lowland pools.

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Order **THYSANOPTERA** Haliday, 1836

(*thysanos*, fringe; *ptera*, wings)

Thrips

Hemiptera, in part, Linnaeus, 1758, and other authors.

Homoptera, in part, Stephens, 1829.

Gymnognatha, suborder *Physopoda* Burmeister, 1838.

Physopoda (Burmeister) Walker, 1852; Comstock, 1888.

Thripsina Newman, 1855.

Physapodes Scudder, 1886.

Small (0.6–14 mm. in length), slender-bodied, spinose insects, usually well sclerotized and pigmented. Head hypognathous or opisthognathous, well exposed, highly modified and specialized, produced below to form a short, pointed beak or *mouth cone*, mouth parts asymmetrical; labrum asymmetrical, forming the front of the beak; clypeus obscure; cephalic sutures obscure or obsolete; mandibles asymmetrical, only the left one developed, the right one obsolete, the left one stylet-like, retractile; maxillae forming the lateral walls of the mouth cone, their palpi two- to eight-segmented, each maxilla bearing a slender, retractile *maxillary stylet*; labium forming the posterior part of the mouth cone, its palpi distal, one- to four-segmented; antennae elongate, longer than the head, filiform or moniliform, six- to nine-segmented, inserted close together on the front of the head between and beyond the eyes; compound eyes prominent, facets large, convex, round; ocelli absent in the immature stages, present or absent in the adults, present in all long-winged forms, present or absent in short-winged forms, when present usually three in number and assembled in a triangle, rarely with only two ocelli. Thorax with all three divisions well developed, prothorax free and movable, pterothorax fused. Legs ambulatory, tarsi unique in structure, one- or two-segmented, with a peculiar protrusible distal vesicle or *bladder* (characteristic of this order only) operated by blood pressure, which enables the insect to cling to and walk over various types of surfaces; with one or two claws, or claws obsolete. Wings four in number, of unique form, long, slender, membranous, not folded, carried overlapping over the abdomen when at rest; with characteristic, long, marginal fringes; veins few or absent, cross-veins rare; wings subject to much modification in form among various species and groups as follows: both sexes may be macropterous, both males and females may have macropterous and brachypterous forms, all may be brachypterous, all males and most females may be brachypterous but some macropterous females may be present, macropterous and apterous males and females may be present, all males may be apterous and the females macropterous, all males may be apterous and some females apterous and some macropterous, and in some forms both sexes may be apterous; when at rest each fore wing in the Terrebrantia rests upon the top of its corresponding hind wing so that the two

pairs lie parallel, but in the Tubulifera the wings are crossed and only one wing is completely visible from above; with at most two longitudinal veins and four or five cross-veins in the fore wings; wing membrane narrow, closely set on the upper surface with microtrichia in the Terrebrantia, but not so clothed in the Tubulifera, with a single row of long flight hairs usually present on the fore margin, the hairs forming a double fringe on the hind margin of the fore wings in the Terrebrantia, but double only near the apices of the fore wings in the Tubulifera; costa of hind wings with several subbasal, hooked spines which catch on a membranous fold on the underside of the fore wing scale when in flight. Abdomen with 10 exposed segments (really 11-segmented), cerci absent, caudal segments cone-shaped in the females, bluntly rounded in most males of the Terrebrantia, but tube-like and bearing a terminal whorl of long setae in the Tubulifera. Three or four pairs of spiracles present, one pair situated at the anterior mesothoracic angles, a pair on the sides of the first and eighth abdominal segments, a fourth pair situated behind the bases of the hind wings on all Tubulifera and some Terrebrantia. Ovipositor present only in the Terrebrantia, situated on the eighth and ninth sternites, curved, saw-like, with four valves, genital openings between the eighth and ninth sternites; female of the Tubulifera with the genital opening between the ninth and tenth sternites, with a heavily sclerotized, small, bar-like structure lying near the hind edge of the ninth sternite, and the basal margin of the tube entire. Males with the sexual aperture between the ninth and tenth sternites, with a copulatory mechanism which can be retracted into the ninth segment; the basal, ventral margin of the tube emarginate in the males of Tubulifera. Parthenogenesis common. Eggs reniform and inserted in plant tissue by most Terrebrantia, elongate-oval and deposited externally in the Tubulifera. Metamorphosis intermediate, but incomplete; two larval molts, followed by a prepupal stage in which the wing pads appear, the pupal stage following the third molt, and in this stage the animal becomes quiescent and has the antennae folded back over the head and the wing pads are elongated; pupation takes place on the host-plant or in the soil. Herbivorous, fungivorous or predaceous; some forms are gall-makers.

Fossil thrips have been described from ambers, copals and shales found in Miocene and Oligocene deposits. According to Essig (1942:253) there are about 2,500 described living species contained in about 350 genera now known. Thrips are an almost cosmopolitan group, and all of the continents are richly supplied with species. Although Australia and adjacent islands have one of the most diversified and rich thrips faunas, it appears that New Zealand has no endemic Thysanoptera.

The word "thrips" is the singular as well as the plural form. The use of "thrip" is incorrect. "Thrips" (masculine) is Linnaeus' original generic name which has come to be used as a common name; it means "wood louse."

There is a decided difference between the upland and lowland thrips faunas in Hawaii. Here, as on the other high islands of Polynesia where I have collected, it is of particular interest that the largest number of Terrebrantia and flower- and

foliage-feeding species is found in the drier, lowland regions—where the immigrant forms predominate—and the fungus-feeding and predaceous Tubulifera of cryptic habits are the ones found most commonly in the wet, highland forest zones. Many of the exposed species appear not to tolerate conditions of heavy rain, but species which are found in trash, under dead bark and in similar protected places are found throughout the mountains, even in the densest rain forests, although many immigrant Terrebrantia are found in the highlands and many are blown high into the mountains by winds and convection currents. However, there are certain Terrebrantia species which prefer the wet-land and forest conditions.

The first paper describing Hawaiian thrips is that by Kirkaldy (1907:102) in which he erected two new genera (*Agnostochthona* and *Nesothrips*) to receive two new species collected near Honolulu. This was followed in 1910 by Bagnall's paper in *Fauna Hawaiiensis* which included Perkins' collection. Almost all the material Bagnall had to work with consisted of dried, card-mounted specimens. Consequently, it has been difficult for subsequent workers to recognize many of his species. Bagnall listed 22 species, of which 15 were described as new. Seven of Bagnall's new species were described from unique specimens, some of them damaged. In 1913 Morgan included a Hawaiian species in one of his papers, but there then followed a lull in Hawaiian thrips studies until 1928 when Moulton published his "Thysanoptera of the Hawaiian Islands" in which 44 species were listed. Since 1928, however, a number of papers on Hawaiian thrips has appeared as new immigrant species have become established, damaged crops, carried plant diseases and aroused local workers to take particular interest in the order.

The order Thysanoptera is most closely allied to the Hemiptera, and, in fact, many authors have included the thrips in that order. The peculiar maxillary stylets are considered by various workers to be analogous to the maxillary forks found in the psocids and to similar structures present in the lice. The feeding mechanism and sucking pump are similar to those of the Hemiptera.

The metamorphosis of thrips is of an intermediate type, and it approaches the complete type in some instances. The larval stage is followed by a prepupal stage, in which the organism can move about but takes no food, and this is followed by a quiescent pupal stage. Some species spin cocoons in which to pupate. Although most species are oviparous, a certain few are known to be ovoviviparous.

Some species crawl slowly about, but others run rapidly; some have a well-developed leaping ability and may jump off their hostplants to take flight. Some species, in both larval and adult stages, have the habit of walking about with the ends of their abdomens curved upward and forward and these forms may resemble small staphylinid beetles.

On the abdomens of some species there are series of spines which are used to arrange the long flight hairs on the wings, and the manipulation of these hairs by curving the abdomen forward is reminiscent of the flexing of the abdomen among the staphylinid beetles. The long flight hairs of the wings, so characteristic of the order, are found only on a few other groups of insects. Certain minute Hymenoptera, Lepidoptera, Trichoptera and a few families of minute Coleoptera

have very slender wings which are armed with a similar type of hair. The hairs serve to extend the wing area to sustain flight. When at rest, the hairs are folded against the wing margins.

Thrips are, in general, gregarious, and they are often found in large colonies on their hostplants. Several or many generations occur each year in Hawaii. Most or all of the life stages usually can be found together at the same time when a colony is examined.

Although certain members of this order are of decided economic importance because they cause severe damage to crops or are vectors of plant diseases, comparatively few of the hundreds of species known are truly detrimental to the interests of mankind. However, the few species that are noxious have given the order a generally bad reputation. Probably most of the known species are feeders on the flowers, leaves and fruits of plants, but others attack the roots, corms and stems. The number of known species which are scavengers, fungivores, carnivores, predators on small arthropods such as aphids, mites and insect eggs is large, and probably a survey would show that the majority of the Pacific species belong to this group. Some species form galls, and especially interesting gall-makers are found in Australia. Some species play a definite part in the pollination of certain plants.

Bailey (1935:856) made a survey of the plant diseases transmitted by thrips. He reported that only two viruses have been clearly demonstrated to be transmitted by thrips, and these are carried by three species of thrips. However, he notes that our knowledge of plant-disease transmission by thrips vectors is at most meager and incomplete. The two diseases mentioned by Bailey are tomato spotted wilt and pineapple yellow spot. Sakimura (1940:281) considers these two diseases to be caused by the same virus. Thrips are also considered to be mechanical vectors of certain bacterial and fungus diseases. Since this was written, Sakimura (1947:57) has published a review of disease transmissions by thrips. He says that spotted wilt is the only virus disease which has been proved to be transmitted by thrips.

The feeding of thrips causes a characteristic type of injury which will be outlined in detail below. New and tender growth is particularly likely to be seriously damaged. The setting of fruit is prevented in some plants when infestation is heavy. Thrips pass copious quantities of liquid feces which dry on the hostplant and cause extensive spotting. When thrips are abundant, parts of the hostplant may become heavily coated with excrement and this may produce an ugly and objectionable discoloration on fruits.

There have been many opinions advanced, and many controversies have arisen, concerning the method of feeding of the Thysanoptera. Some of these have been summarized by Wardle and Simpson (1927:513) as follows:

Thus the thrips has been stated to puncture the tissues and drain the contents of the cells, causing the cell walls to collapse (Horton, J. R. 1921, re *Scirtothrips citri* Moul.); to pierce the epidermis and rasp away the leaf tissues within (Russell, H. M. 1912, re *Heliothrips rubro-cinctus* Giard.); to rasp the leaf tissues and suck up the sap as it exudes (Bedford, H. W.

1921, re *Heliothrips indicus* Bagn.); to pierce the vegetable tissue with its stylets and suck up the liberated plant juices (Cameron, A. E. and Treherne, R. C. 1918, re *Taeniothrips inconsequens* Uzel).

Wardle and Simpson studied *Thrips tabaci* in detail, and their conclusions (1927: 527) are as follows:

1. Observations and experiments concerning *Thrips tabaci* on cotton and other plants suggest that plant injury from thrip[s] attack is in this case due entirely to premature and excessive defoliation, and is dependent in extent and severity upon the value of the infestation factor, or number of thrip[s] stages per unit area of foliage surface. Differences between plant species, plant varieties and plant individuals as regards susceptibility to injury arise chiefly through variations in thickness of the epidermal cell layer.

2. Leaf injury consists essentially of necrosis of a patch of mesophyll cells lying immediately below a gash in an epidermal cell. Such necrosed patches are scattered and isolated when the infestation factor is low, but are confluent and form extensive rusty areas when the infestation is high. Such areas consist of dead cells of the superficial mesophyll layers; the deeper layers, palisade tissue and epidermal layers remain intact, except for the initial gashes made in epidermal cells. In later stages of leaf injury, such necrosis involves the whole leaf, all the layers become disorganized, and premature shedding occurs. There is no evidence that the insect salivary secretion is toxic.

3. The insect does not puncture or rasp the epidermis but gashes an epidermal cell by pickaxe-like movements of the single mandible, induced by a slight rocking movement of the head. In most cases, the mandible can only gash the outer epidermal wall, the inner wall and the lateral walls of the mesophyll cells being broken down by similar movements of the longer protruded maxillary laciniae. There is no evidence of attack through the stomata. Suction of the chloroplasts into the pharynx is aided probably by the partial vacuum established within the mouth cone when applied closely to the leaf surface.

4. The preference shown by thrip[s] stages for the lower surface of leaves is believed to be due rather to differences in thickness of epidermis between the lower surface and the upper surface, than to negative phototropism. In plants where such differences are slight, such as cotton plants, thrip[s] stages readily invade the upper leaf surface. On *Cajanus indicus*, the upper surface is the more favoured, the lower surface being unsuitable owing to the close spacing of numerous fine hairs. The more widely spaced hairs on cotton leaves do not act as a deterrent, the hairy American and Indian varieties being more heavily attacked than the smoother leaved Egyptian varieties of cotton.

However, Hinds (1902:117) stated that at least some species would move to the dark side of a leaf if it were turned over so as to expose the thrips to direct light. Additional notes on feeding are given under *Thrips tabaci* in this text.

Field workers and agriculturists are frequently bitten by thrips, especially in areas of heavy infestation. Some Thysanoptera will actually feed on man by puncturing the skin and sucking blood. I have been bitten by thrips on a number of occasions, but only a slight, sharp, pricking sensation was noted. Some people have reported swellings, itching and a "pinkish dotting" of the skin at the site of the bites. Bailey (1936:95-98) gives a good summary of thrips attacking man, and his report includes a bibliography.

There are a number of insect enemies of thrips. Among the predators are *Orius* and related anthorcid bugs, chrysopid lacewings, syrphid fly larvae and coccinellid beetles. *Orius persequens* is a common predator in Hawaii. Illing-

worth (1931:879) reported that the abundant cucujid beetle, *Cryptomorpha desjardinsi*, was a thrips predator both in the larval and adult stages. In Hawaii, the immigrant, minute, remarkable, fringe-winged, trichogrammatid wasp, *Megaphragma mymaripenne* Timberlake (Timberlake, 1924:414), attacks the eggs of some species, including *Heliothrips haemorrhoidalis*. Two species of small, tetrastichine, chalcid wasp parasites of larvae have been imported. One, *Thripoctenus russelli* Crawford (see Russell, 1912:1), has been purposely brought in from California, and the other, *Thripoctenus brui* Vuillet, was introduced from Japan to prey upon *Thrips tabaci*. These last two parasites lay their eggs in the bodies of the larval thrips, and the parasites subsequently destroy their hosts. In addition to insect enemies, certain nematode worms, fungi, mites and spiders are known to attack thrips.

As noted above, the Terrebrantia are generally not tolerant of wet, rainy conditions, and inasmuch as our principal crop-pest thrips belong to this suborder, heavy rains are a decided aid in reducing and keeping down thrips populations. The worst thrips damage can be expected to occur in the drier, hotter regions of our islands.

The artificial control of thrips consists principally of dusting and spraying. Nicotine dusts and sprays have been long used successfully, and tartar emetic-sugar-water sprays are gaining favor among many growers. Further information on control is given under the species headings.

The Thysanoptera are largely in a state of taxonomic chaos, and the group is a most difficult one to work with systematically. There is not yet available a classification which can be considered adequate or natural. The basic concept of what constitutes the various categories of classification appears more often than not to have been lost sight of. Few authorities agree as to what constitutes a genus, subfamily, family or superfamily. Speyer (1934:150-151) expressed his opinion as follows:

At least amongst the Thysanoptera, the ever-growing confusion is due to meagreness of description for the generic character. However true the contention that the genus is a group of somewhat similar species, assembled together for the sake of convenience rather than philogenetic affinity, there is no justification for a system of classification based upon structures of the insect which happen conveniently to strike the eye, with no primary inquiry into the possibility of such structures being highly variable in the species. The scientific examination of structure has of late given way to short-cut methods of mechanical measurement, relating to portions of the external anatomy for which no attempt at proof of constancy in the species has been undertaken.... The confusion that has arisen can be unravelled only by reference to the *type species* of such genera as have already been raised, for these are the only definitely *fixed points* which are available to the systematist.

In not a few cases the actual type specimen representing the genus may not be available, or is in a state of preservation which defies examination, but in the majority of cases the *type* of the genus is represented by a species not only well recognised, but of which fresh material can without difficulty be obtained. There is now occasion for the systematist to determine from series of specimens what characters are liable to most and what characters to least variation in the type species of each genus, and from the latter category and from a similar examination of related species to choose constant characters which are serviceable for the separation of species within the genus. Only after such an undertaking is complete

will it be possible to raise genera and higher groups for the final constitution of a justifiable classification, of practical value for the systematist and satisfactory to the needs of the biologist.

Newly emerged individuals differ, as other insects do, from fully matured individuals. Yet new forms are described from teneral specimens. One author placed specimens of one species in two different genera, because one lot was col-

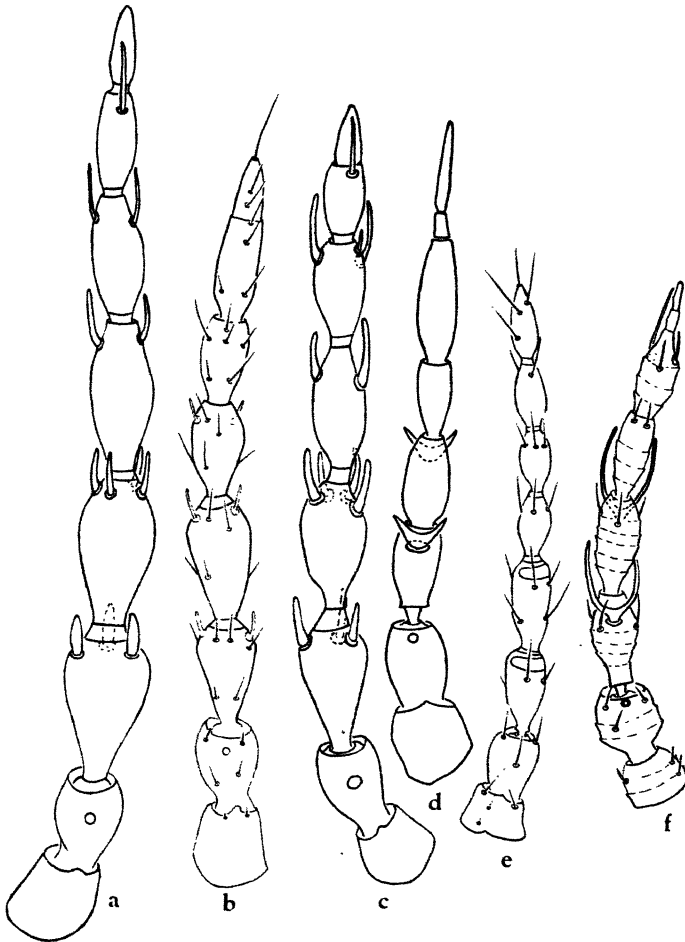


Figure 216—Sketches of the antennae of some thrips. a, *Phlaeothrips claratibia* Moulton; b, *Hoplothrips flavipes* (Bagnall); c, *Hoplothrips mauiensis* Moulton, paratype male; d, *Docidothrips trespinus* (Moulton), female, right dorsal; e, *Merothrips hawaiiensis* Moulton, female, right dorsal; f, *Dendrothripoides ipomeae* Bagnall, female, right dorsal. (Kindly drawn for this chapter by F. A. Bianchi.)

lected in a cyanide bottle and allowed to dry up before being placed in alcohol, whereas the other lot from the same plant was placed directly from the hostplant into alcohol. The proportions of the heads of the dried specimens differed from the measurements of the examples preserved in fluid. For a discussion of the confusing variability in a single species, see the discussion under *Taeniothrips hawaiiensis* farther along in this section.

In the following text, I have attempted to follow the classification and methods of distinguishing the various groups that are in current use, but I have not always been successful. I feel that much work remains to be done before even our small thysanopterous fauna is satisfactorily arranged taxonomically, and I know that the following text needs much revision. However, it has been my purpose to try to present materials which will enable the struggling worker to identify his collections of Hawaiian specimens.

I am indebted to Dr. Frederick Laing for sending notes on the Bagnall types in the British Museum which are incorporated herein.

TABULAR ANALYSIS OF THE HAWAIIAN THYSANOPTERA

FAMILY	GENERA	ENDEMIC GENERA	NON- ENDEMIC GENERA	SPECIES	ENDEMIC SPECIES	ADVENTIVE SPECIES
Aeolothripidae	1	0	1	1	0	1
Thripidae	20	0	20	46	7(?)	39
Phlaeothripidae	14	1(?)	13	39	14+6(?)	15+4(?)
Urothripidae	2	1	1	2	1	1
Totals	37	2(?)	35	88	28(?)	60(?)

Percentage of endemism in native group: genera, 33.3 percent (?); species, 100 percent.

Percentage of present-day fauna native: 31.5 percent.

Percentage of present-day fauna adventive: 68.1 percent.

Average number of species per genus in native group: 4.6.

Average number of species per genus in adventive group: 1.7.

These figures will be subject to change when our thrips fauna has been revised and studied in detail. The status of a number of the species is uncertain.

KEY TO THE SUBORDERS

1. Wings with well-developed veins, fore pair with a marginal vein and at least one longitudinal vein that reaches apex; wing membrane with microscopical hairs; terminal abdominal segment sub-conical in female, broadly rounded in male, never tubular; ovipositor present and saw-like. **Terrebrantia.**
2. Wings with greatly reduced venation, fore pair with at most only a median longitudinal vein that does not reach the wing apex; wing membrane without minute hairs; terminal abdominal segment tubular in both sexes, often conspicuously elongate; ovipositor absent **Tubulifera.**

Suborder TERREBRANTIA Haliday, 1836

This suborder contains the more important crop-pest thrips. Its members are mostly more active than those of the Tubulifera and generally have less cryptic habits. Many species are found on flowers and many are active runners and/or jumpers.

The apex of the abdomen of the females is usually pointed and sub-cone-shaped, whereas it is usually bluntly rounded in the males. The ovipositor is normally well developed. It has four valves, is saw-like, and usually lies partially or completely concealed in a sheath in the three terminal ventrites when at rest.

KEY TO THE SUPERFAMILIES OF TERREBRANTIA

1. Wings comparatively broad, apices rounded; antennae nine-segmented; ovipositor curved upward; body not depressed **Aeolothripoidea.**
2. Wings comparatively narrow, apices usually pointed; antennae six- to eight-segmented; ovipositor curved downward; body somewhat depressed **Thripoidae.**

Superfamily AEOLOTHRIPOIDEA Hood, 1915

This superfamily contains only one family, and it includes the most primitive of the known living Thysanoptera.

Family AEOLOTHRIPIDAE Uzel, 1895

Antennae nine-segmented, either freely movable or with the apical joints connate; intermediate segments usually cylindrical, without specialised chaetotaxy, but uniformly clothed with short setae. No sense-cones present; membranous, longitudinally elongated sensory areas on segments three and four, and smaller areas on certain other segments. Maxillary palpi geniculate, 3-8 segmented; labial palpi 2-5 segmented. Wings, when present, large, broad and rounded apically; forewing with a heavy ring-vein [the ambient or marginal vein] and two longitudinal veins reaching from base to tip and each uniting with the ring-vein before tip; cross veins usually present; front margin of forewings without, or with only a light fringe of hairs. Legs long. Ovipositor curved backwards. (Bagnall, 1913:394.)

Subfamily AEOLOTHRIPINAE Bagnall, 1913:396

The Broad-Winged Thrips

Genus AEOLOTHRIPS Haliday, 1836:451

Aeolothrips fasciatus (Linnaeus) (fig. 217, a).

Thrips fasciata Linnaeus, 1758:457; 1761:267.

For detailed description and illustrations, see Hinds, 1902:127-130. For synonymy and description, see Priesner, 1928:105.

Genotype of *Aeolothrips*.

The striped or banded thrips; the six-spotted thrips.

Oahu, Maui, Hawaii.

Immigrant. Cosmopolitan. First found in the Hawaiian Islands by Swezey on *Styphelia* (*Cyathodes*) *tameiameiae* on Mount Haleakala, Maui, in 1927.

This species, whose fore wings have a pale cross band at base, middle and apex, with broader dark brown bands between the white bands, can be expected to be found on many plants. It preys upon other thrips, aphids, mites, etc., and it spins a cocoon in which to pupate.

Superfamily THRIPOIDEA Hood, 1915:57

Several families are recognized in this division, but representatives of only one are known to occur in Hawaii.

Family THIRIPIDAE Uzel, 1895

The members of this family have from six to eight segmented antennae... the segments beyond the sixth are usually short and form what is called the style. Maxillary palpi are usually three, sometimes two segmented; labial palpi never composed of more than two segments. The wings of Thripidae are usually slender, gradually tapering more or less and pointed at the tips. The fore wings, as a rule, present two parallel longitudinal veins, the front one running from the base to near the tip of the wing; the hind vein appears usually as a branch from the fore vein at about one-third the length of the wing. Sometimes, however, all connection between these veins is wanting. Cross veins are rarely visible, though traces of them can sometimes be seen. The ring vein is not usually very heavy or prominent. A fringe is generally present upon the front margin of the fore wing, but may be vestigial. More or less stout spines are found along the veins and costa of the fore wing. The hind wing has one median, longitudinal vein without spines and no cross or ring veins, but the costa bears a fringe. The ovipositor of the female is bent downward, i.e., concave side ventral. (Hinds, 1902:132.)

KEY TO THE SUBFAMILIES FOUND IN HAWAII

1. Antennae inserted on a triangular process which is drawn out in front of eyes; males apterous, females winged. **Chirothripinae.**
Front of head not so produced; sexes usually, but not always, similar 2
- 2(1). Derm, especially of head and prothorax, with conspicuous, deep, coarse, polygonal, reticulate sculpture **Heliothripinae.**
Derm not so sculptured (at most with partially confluent, transverse wrinkles forming a fine reticulation) 3
- 3(2). Fore wings with only one longitudinal vein (but compare Thripinae); prothorax for the most part without long spines **Sericothripinae.**

Fore wings with two or more longitudinal veins (except in *Leucothrips* in which the two longitudinal veins in fore wings are fused from near base to apex); at least the hind angles of prothorax with rather long spines (except in *Anaphothrips*) **Thripinae.**

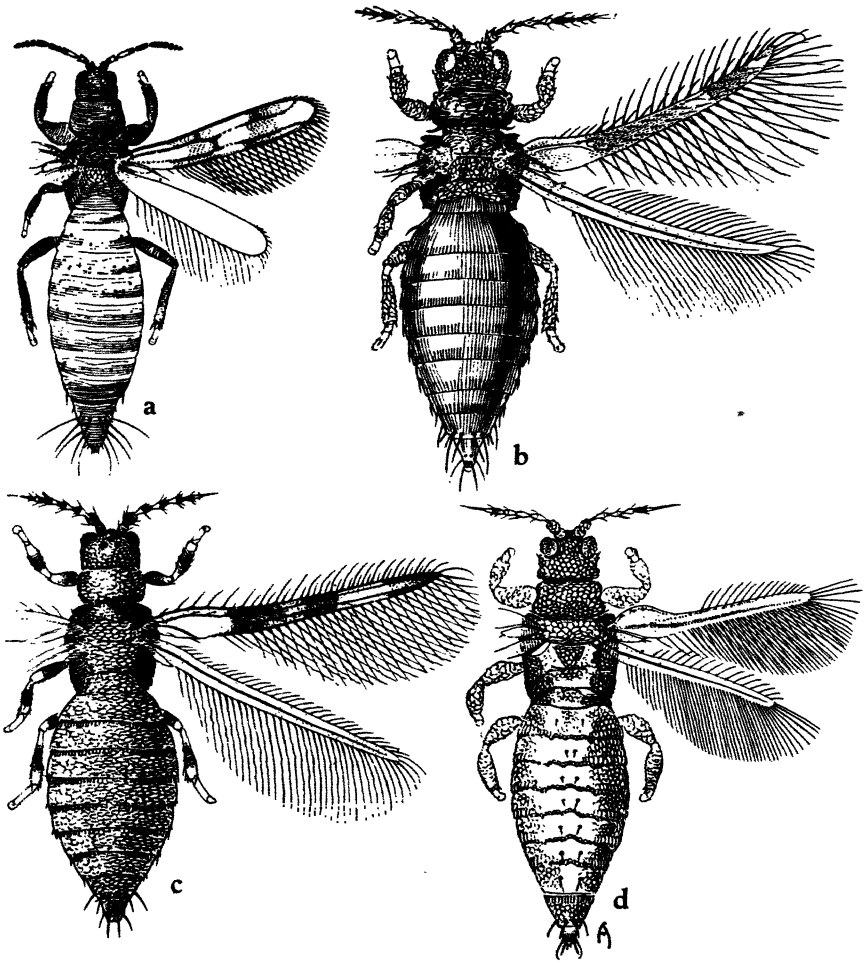


Figure 217—**a**, *Aeolothrips fasciatus* (Linnaeus); **b**, *Hercinothrips femoralis* (Reuter); **c**, *Hercothrips fasciatus* (Pergande); **d**, *Heliothrips haemorrhoidalis* (Bouché). (Abernathy drawings; not to same scale.)

Subfamily HELIOTHIRIPINAE Karny, 1921

KEY TO THE GENERA FOUND IN HAWAII

1. Head with a collar near hind margin in front of basal constriction, showing as a dentiform process at either side at postero-lateral angles (the collar may be difficult to see, but the processes are distinct) **Hercinothrips** Bagnall.
Head without such a collar or processes..... 2
2. Antennal segments three and four stem-like at either end and with forked trichomes; hind coxae less than one-third as widely separated as breadth of a coxa..... **Hercothrips** Hood.
Antennal segments three and four not stem-like at the distal ends and without trichomes; hind coxae fully one-half as widely separated as breadth of a coxa..... **Heliothrips** Haliday.

Genus **HERCINOTHIRIPS** Bagnall, 1932:506**Hercinothrips femoralis** (Reuter) (fig. 217, b).*Heliothrips femoralis* Reuter, 1891:166.*Hercinothrips femoralis* (Reuter) Bagnall, 1932:506.

Redescribed and figured by Hinds, 1902:172, pl. 5, figs. 55-56; pl. 6, fig. 57.

For synonymy see Priesner, 1928:130.

The banded greenhouse thrips.

Kauai, Oahu, Maui, Hawaii.

Immigrant. A widespread species. First recorded from the Hawaiian Islands by Moulton (1934:499) from specimens collected by Sakimura in Honolulu.

Hostplants: banana (causes "silver and bronze scars" which may result in damage of some economic importance), beet, celery, *Commelina diffusa* (*nudiflora*), *Crinum*, *Chrysanthemum*, dwarf milo maize, eggplant, *Emilia sonchifolia* (*flammea*), *Erechtites hieracifolia*, grass, orchids, pineapple, *Plantago major*, *Sonchus oleraceus* ("pualele," sow thistle), sugarcane, tomato.

For a list of hostplants in America see Eide, 1943:327. For notes on damage done to bananas, see Bianchi, Proc. Hawaiian Ent. Soc. 12(3):481, 1946.

Control: nicotine sulphate in 1:400 to 600 dilution has been recommended for use on orchids.

Genus **HERCOTHIRIPS** Hood, 1927:233**Hercothrips fasciatus** (Pergande) (fig. 217, c).*Heliothrips fasciata* Pergande, 1895:391.*Hercothrips fasciatus* (Pergande) Hood, 1927:233.

See Bailey (1933) for bionomics (in California), for detailed descriptions of all stages, illustrations, bibliography, etc.

The bean thrips.

Oahu, Molokai, Hawaii.

Immigrant. Widespread. First found in the Hawaiian Islands by Krauss at Kaunakakai, Molokai, in June, 1943, and by Bianchi on Hawaii in June, 1945, and Oahu in April, 1946.

Hostplants: *Argemone alba* var. *glauca* (leaves, flowers, buds), *Sonchus oleraceus*. (Possible hosts which may be attacked in Hawaii include alfalfa, avocado, bean, beet, cabbage, cauliflower, corn, cotton, grape, lettuce, nasturtium, onion, citrus, pea, potato, radish, Swiss chard, tomato, turnip, *Amaranthus*, *Bidens*, *Cassia*, *Erigeron* and *Nicotiana glauca*.)

This species has become established in Hawaii so recently that no survey of its habits has been made here. However, it is a serious pest elsewhere, and it is most unfortunate that it has established itself in Hawaii. Essig (1929:183) says that it "is a general feeder on leguminous plants, truck, field and forage crops, grasses, deciduous and citrus fruit trees, and so forth, and is a serious pest to beans and cotton in California and Arizona, and to the fruits of oranges, avocados and olives in California." It is an important pest to commercial crops in the dry and non-irrigated parts of California. The species was originally described from Yuba County, California.

The females can reproduce parthenogenetically, but in doing so are capable of giving rise only to males. Females can only be produced by fertilized females.

This species is an active jumper—being capable of leaping about a foot—but it is not a strong flyer. Pupation takes place in the soil.

Parasite: *Thripoctenus russelli* Crawford (Hymenoptera: Eulophidae).

Genus **HELIOTHRIPS** Haliday, 1836:443

Heliothrips haemorrhoidalis (Bouché) (fig. 217, d).

Thrips haemorrhoidalis Bouché, 1833:206.

Heliothrips Adonidum Haliday, 1836:443. Genotype.

For detailed synonymy and description, see Hinds, 1902:168, and Priesner, 1928:126.

The greenhouse thrips.

Kauai, Oahu, Molokai, Maui, Hawaii.

Immigrant. Almost cosmopolitan. First recorded from Hawaii by Bagnall (1910:698) from specimens collected by Perkins.

Hostplants: boysenberry, *Clermontia parviflora*, croton, *Eucalyptus* (damaging young leaves), *Fuchsia*, *Gladiolus*, *Hibiscadelphus giffardianus* (found damaging seriously the last known example of this nearly extinct native tree), *Hibiscus*, *Hypochaeris radicata*, *Metrosideros*, peach, *Rubus penetrans*, *Uaccinium calycinum*.

Probably also on: *Araucaria*, avocado, azalea, bignonia, citrus, fig, guava, *Pelea*, *Rhododendron*, rose, *Styphelia*.

Parasite: *Megaphragma mymaripenne* Timberlake (1924:414, fig. 7) (Hymenoptera: Trichogrammatidae) on the eggs (the exit holes, 0.08–0.09 mm. in diameter, may be seen in the swellings in the leaves over the thrips eggs).

The greenhouse thrips has been the cause of considerable injury to ornamentals during the past century, and where its presence is not suspected or treatment is neglected it will cause the utter ruin of certain plants, in the greenhouse, grown principally for the beauty of their foliage. Likewise in the more tropical sections of the United States, such as southern Florida and southern California, this insect causes great damage to some outdoor plants. (Russell, 1912:1.)

No detailed studies have been made on this species in Hawaii, although it has been here for many years. The feeding punctures appear to be confined largely to the foliage, with the fruits of some kinds of plants similarly attacked. Russell (1912) found the egg stage to be of about eight days' duration, the larval period 10 to 20 days, and the prepupal–pupal periods four to six days. The entire life cycle may take from three weeks to one month. Only females of this species are known, and all reproduction is parthenogenetic. The larvae pupate on the host.

The foliage and fruits of attacked plants become heavily spotted with excrement and may become conspicuously discolored.

Control: tartar emetic–sugar–water sprays have been recommended.

Wittwer and Haseman (1946:331) noted in their experiments that New Zealand spinach grown with a high nitrogen supply was almost immune to attack, whereas plants grown with a low nitrogen supply were heavily attacked.

Subfamily SERICOTHRIPINAE Karny, 1921

KEY TO THE GENERA FOUND IN HAWAII

1. Maxillary palpi two-segmented; fore wings very narrow, veins obsolete **Dendrothripoides** Bagnall.
Maxillary palpi three-segmented; fore wing veins distinct 2
2. Eyes comparatively prominent and protruding; antennal segments five and six closely joined, six sub-cone-shaped
..... **Scirtothrips** Shull.
Eyes not prominent, not protruding; antennal segments five and six not closely joined, six sub-spindle-shaped
..... **Anaphothrips** Uzel.

Genus **DENDROTHRIPOIDES** Bagnall, 1923:624

Dendrothripoides ipomeae Bagnall (figs. 216, f; 218).

Dendrothripoides ipomeae Bagnall, 1923:625. Genotype.

Kauai, Oahu.

Immigrant. Almost cosmopolitan; described from India. First found in Hawaii at Kailua, Oahu, by Bianchi in 1941.

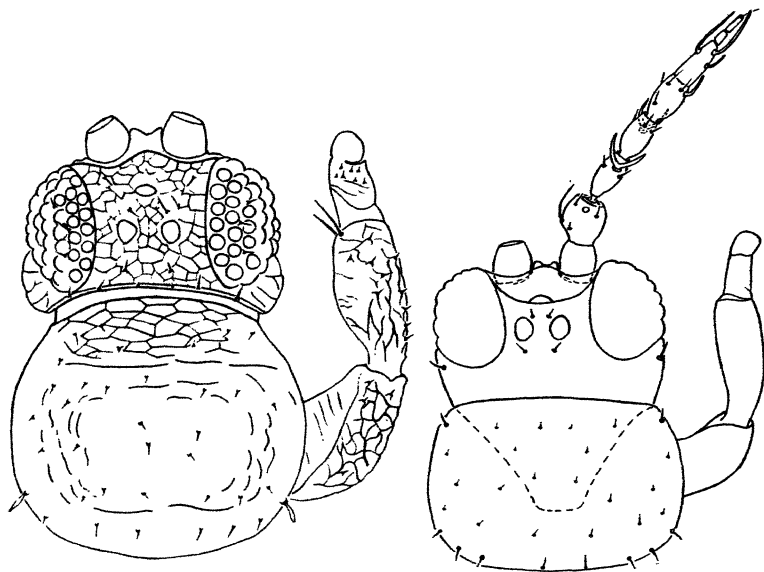


Figure 218—Details of two thrips: *Dendrothripoides ipomeae* Bagnall, left; *Scirtothrips antennatus* Moulton, right. (Kindly drawn for this text by F. A. Bianchi.)

Hostplants: *Echinochloa crus-galli*, *Dioscorea*, *Ipomoea congesta*, lettuce, sweet potato.

Although this species has been reported to cause damage to sweet potatoes here and abroad, Bianchi (who found the eggs inserted just under the surface of tender new shoots) reported in 1942 that he found no damage to sweet potatoes, but, on the contrary, there appeared to be some indication that the species was preying on the eggs of the leaf miner *Bedellia orchilella* Walsingham. However, Sakimura and Nishida (1944:125) record definite damage to sweet potato and lettuce, and Look and Nishida (Proc. Hawaiian Ent. Soc. 12[2]:216, 1945) report severe damage to sweet potatoes. "The injured leaves are scarred and crinkled by the thrips which breed in the young shoots. This injury is easily confused with that of the broad mite, *Hemitarsonemus latus* (Banks)."

Genus **SCIRTOTHRIPS** Shull, 1909

Scirtothrips antennatus Moulton (fig. 218).

Scirtothrips antennatus Moulton, 1937:409.

Kauai, Oahu (type locality: Honolulu), Hawaii.

Immigrant from North America.

Hostplants: burdock, *Colubrina oppositifolia*, carrot, cowpea, *Nothopanax*, parsley, *Passiflora*, *Plumeria*.

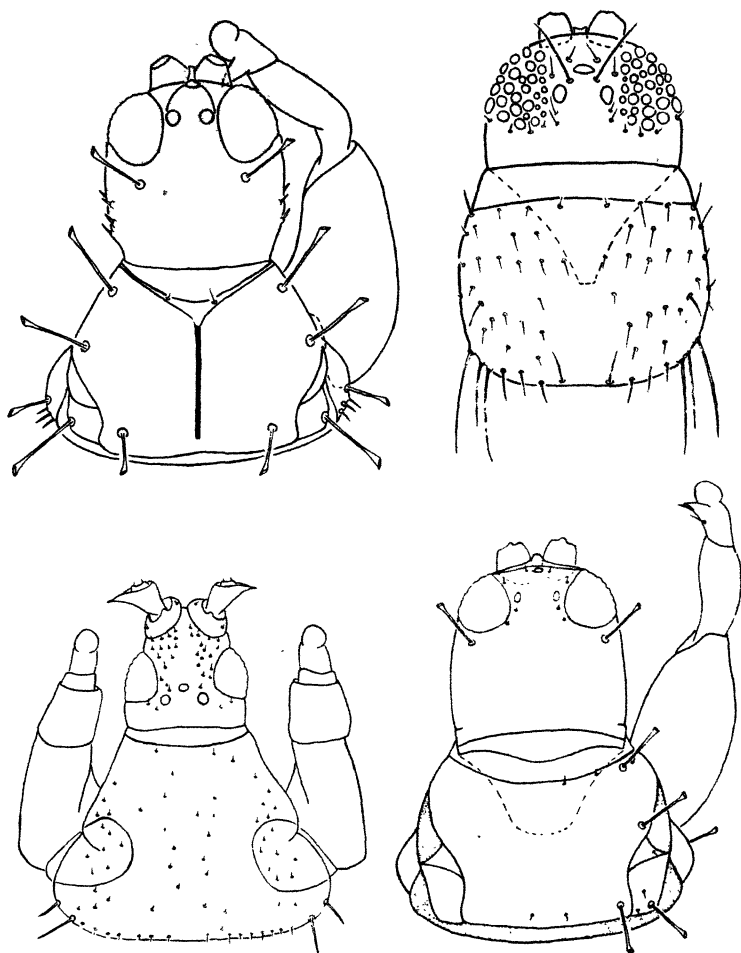


Figure 219—Details of some thrips. Top left, *Phlacothrips mauiensis* Moulton, paratype male, minor setae omitted; top right, *Docidothrips trespinus* (Moulton); bottom left, *Chirothrips fulvus* Moulton; bottom right, *Hoplothrips flavipes* (Bagnall). (Kindly drawn for this work by F. A. Bianchi.)

Genus **ANAPHOTHRIPS** Uzel, 1895:142

KEY TO THE SUBGENERA

1. Prothorax without long bristles on hind margin; sixth antennal segment less than three times as long as broad in our species; fore wings not banded **Anaphothrips** Uzel.
2. Hind margin of prothorax with long bristles; sixth antennal segment more than three times as long as broad in our species; fore wings with two dark bands. . . . **Chaetanaphothrips** Priesner.

Subgenus *Chaetanaphothrips* Priesner, 1924:145; 1928:204

Anaphothrips (*Chaetanaphothrips*) *orchidii* (Moulton) (fig. 220, a).

Euthrips orchidii Moulton, 1907:52, pl. 2, fig. 15-18.

Anaphothrips (*Chaetanaphothrips*) *orchidii* (Moulton) Priesner, 1924:145; 1928:204. Type of subgenus.

Kauai, Oahu, Hawaii.

Immigrant. Widespread. First recorded from the Hawaiian Islands by Moul-

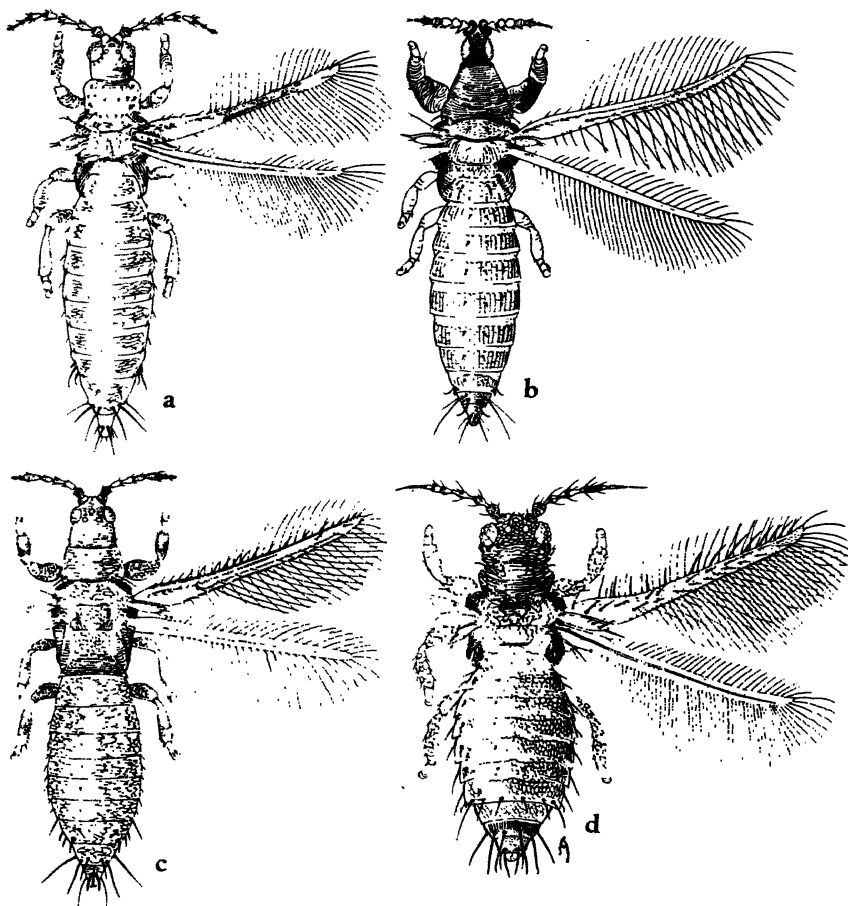


Figure 220—*a*, *Anaphothrips orchidii* (Moulton); *b*, *Chirothrips mexicanus* Crawford; *c*, *Limothrips cerealium* (Haliday); *d*, *Selenothrips rubrocinctus* (Giard). (Abernathy drawings; not to same scale.)

ton (1928:107) from a specimen collected by Williams from *Commelina diffusa* (*nudiflora*) on Mount Tantalus, Oahu.

Hostplants: *Anthurium*, *Bougainvillea*, *Commelina diffusa* (*nudiflora*), *Emilia sonchifolia*, grass, *Heimerliodendron brunonianum*, *Litchi*, orchids (with occasional heavy infestations reported), parsley, sweet potato.

Takahashi (1936:430) reports that this species rolls the edges of young leaves of a species of *Machilus* in Formosa. It is a parthenogenetic form, and no males have been found in Hawaii. Sakimura has found that a complete life cycle on *Emilia sonchifolia* takes less than 33 days in the winter months in Hawaii.

Subgenus *Anaphothrips* Uzel

KEY TO THE SPECIES KNOWN TO OCCUR IN HAWAII

1. Dark-brown species **secticornis** (Trybom).
Pale-yellow species 2
2. Spines on dorsal apical margin of precaudal (ninth) abdominal tergite dark, heavy, stiff **obscurus** (Müller).
Spines on dorsal apical margin of ninth tergite pale, thin, slender **swezeyi** Moulton.

Anaphothrips (*Anaphothrips*) **obscurus** (Müller).

Thrips obscurus Müller, Zool. Dan. Prodröm, p. 96, 1776 (I have not seen this reference).

Anaphothrips (*Anaphothrips*) *obscurus* (Müller), Priesner, 1928:183.

Oahu, Maui.

Immigrant. Nearly cosmopolitan. First found in the Hawaiian Islands in 1944 by Bianchi in a greenhouse at Honolulu (1945:282).

Hostplants: Sudan grass, sugarcane.

"On Sudan grass the damage appeared in the usual 'silvering' of the leaves while on young cane the edges of the leaves become red or reddish in longitudinal areas and partly curled back upon themselves." (Bianchi, 1945:283.) This is a grass pest species elsewhere.

Anaphothrips (*Anaphothrips*) **secticornis** (Trybom).

Thrips secticornis Trybom, Öfv. Vet. Akad. Förh. 8(8):620, 1896 (I have not seen this publication).

Anaphothrips (*Anaphothrips*) *secticornis* (Trybom), Priesner, 1928:189, fig. 42.

Hawaii.

Immigrant. A widespread Holarctic species. First found at Kilauea, Hawaii, by Bianchi in 1944 (1945:282).

Hostplant: barley (?).

Anaphothrips (Anaphothrips) swezeyi Moulton.

Anaphothrips (Anaphothrips) swezeyi Moulton, 1928:107.

Kauai, Oahu (type locality: Honolulu), Hawaii.

Immigrant, but not yet recorded elsewhere.

Hostplants: a common grass thrips; *Cenchrus echinatus*, *Digitaria sanguinalis* (*Syntherisma sanguinalis*), *Echinochloa crus-galli*, *Panicum purpurascens* (*barbinode*), *Panicum torridum*, *Setaria geniculata* (*Chaetochloa geniculata*), *Setaria verticillata* (*Chaetochloa verticillata*), sugarcane, *Tricholaena repens* (*rosea*), *Trisetum glomeratum*.

This species appears to be closely similar to *obscurus*, and the differences between it and *obscurus* are hard to describe. Perhaps it is not a distinct species.

Subfamily CHIROTHRIPINAE Karny, 1921

KEY TO THE GENERA FOUND IN HAWAII

1. Prothorax almost twice as long as head; second antennal segment remarkably expanded on outer side. . **Chirothrips** (Haliday).
Prothorax not much longer than head; second antennal segments not so formed 2
2. Antennae six-segmented **Aptinothrips** Haliday.
Antennae eight-segmented **Limothrips** (Haliday).

Genus **CHIROTTHRIPS** (Haliday)

Thrips, subgenus *Chirothrips* Haliday, 1836:444.

The males of all the species are apterous.

KEY TO THE SPECIES FOUND IN HAWAII

1. Basal abdominal tergites with subbasal serration or lobes; forehead with two pairs of setae on each side between anterior ocelli and base of antennae, and a seta on each side between anterior ocelli and base of antennae and a seta on either side of anterior ocellus..... **mexicanus** Crawford.
Basal abdominal tergites not serrate; forehead with four or more setae anterior to fore ocellus..... 2
2. Forehead with about four to eight setae on each side, none opposite anterior ocellus..... **spiniceps** Hood.
Forehead with about 15 to 17 setae on each side, with one on each side of anterior ocellus..... **fulvus** Moulton.

Chirothrips fulvus Moulton (fig. 219).

Chirothrips fulvus Moulton, 1936:182.

Kauai, Oahu (type locality: Paumalu), Hawaii.

Immigrant; also known from Texas (material in Moulton collection).

Hostplants: *Paspalum orbiculare*, *Paspalum dilatatum* (Dallas grass).

"This species is distinguished by having fifteen to seventeen forehead setae [on each side, that is] and the ocellar pair placed opposite anterior ocellus, by the enlarged first antennal segments, fore wings with light bands also the fore vein of fore wing has four spines near base and two near tip; the hind vein has five rather regularly placed spines." (Moulton, 1936:183.)

Chirothrips mexicanus Crawford (fig. 220, b).

Chirothrips mexicanus Crawford, 1909:114, fig. 51.

Moulton, 1928:106, describes the male.

Kauai, Oahu, Maui, Hawaii, Midway.

Immigrant. Known from North and South America and the Philippines. First recorded from the Hawaiian Islands by Moulton (1928:106) from specimens collected on Oahu by Swezey in 1927. Described from tobacco flowers from Guadalajara, Mexico.

Hostplants: *Ammophila arenaria*, *Chloris inflata* (*paraguayensis*). *Eragrostis variabilis*, *Panicum purpurascens*, *Setaria geniculata*, sugarcane.

This species has only two pairs of forehead setae on each side and one seta at either side of the anterior ocellus; there is one longitudinal vein in the fore wing, the first antennal segment is deep brown; there is a pair of heavier and distinctly differentiated spines on the postero-lateral prothoracic angles, and the basal abdominal tergites are subbasally serrate.

Bianchi (1941:37) reported finding the species in large colonies on *Eragrostis variabilis* and *Ammophila arenaria* on Midway Island.

Chirothrips spiniceps Hood.

Chirothrips spiniceps Hood, 1915:12, pl. 1, fig. 8.

Chirothrips sacchari Moulton, 1936:181. Synonymy by Hood, 1939:464.

Kauai, Oahu.

Immigrant. A widespread North American species. First recorded from the Hawaiian Islands by Moulton (1936:181) from specimens collected at Kailua, Oahu, by Swezey.

Hostplants: corn, *Setaria geniculata*, *Echinochloa crus-galli* (barnyard grass), sugarcane.

This species has four to eight forehead setae on each side; two longitudinal wing veins; the first antennal segment is yellow or slightly infuscated and the pair of spines on the postero-lateral corners of the prothorax is not strongly differentiated from its neighbors. It has not caused any particular damage in Hawaii, although it is at times quite abundant locally.

Genus **APTINOTHRIPS** Haliday, 1836**Aptinothrips rufa** (Gmelin).*Thrips rufa* Gmelin, in Linnaeus, 1788:2224.

Maui, Hawaii.

Immigrant. A widespread species described from Europe. First found in the Territory by Bianchi at Kilauea, Hawaii, in 1944 (1945:282).

Hostplants: barley (?), "grass," *Holcus lanatus*.Genus **LIMOTHRIPS** (Haliday)*Thrips*, subgenus *Limothrips* Haliday, 1836:444.**Limothrips cerealium** (Haliday) (fig. 220, c).*Thrips (Limothrips) cerealium* Haliday, 1836:445.*Limothrips avenae* Hinds, 1902:139, pl. 1, figs. 10-12; pl. 2, fig. 13.

The cereal or corn thrips.

Kauai, Oahu, Hawaii.

Immigrant. Cosmopolitan. First recorded from the Hawaiian Islands by Bag-nall (1910:701) from specimens collected by Perkins in 1892 and 1897.

Hostplants: various grasses.

Hinds (1902:139) gives a detailed, illustrated description of this species. The males are apterous.

Subfamily **THRIPINAE** Karny, 1921

This subfamily contains most of the thrips of economic importance.

KEY TO THE GENERA FOUND IN HAWAII

1. Antennae thread-like, eight-segmented, without a terminal style; pronotum with longitudinal dorsal sutures; fore and hind femora conspicuously swollen. . . . **Merothrips** Hood.
- Antennae not thread-like, six- to eight-segmented with a terminal one- or two-segmented style; pronotum without longitudinal dorsal sutures; fore and hind femora not swollen 2
- 2(1). Derm with numerous, confluent, sculpture ridges forming a fine reticulation **Selenothrips** (Karny).
- Derm not so reticulated. 3
- 3(2). Antero-lateral prothoracic angles armed with one or more long, strong bristles 4
- Antero-lateral prothoracic angles not so armed. 5
- 4(3). Lateral margins of prothorax each with a comparatively long bristle at middle; interocellar bristles as long as or longer than head; wings with dark maculae. **Scolothrips** Hinds.

- Lateral prothoracic margins without such bristles; inter-
 ocellar bristles shorter than head; wings pale.....
**Frankliniella** Karny.
- 5(3). Maxillary palpi two-segmented 6
 Maxillary palpi three-segmented 7
- 6(5). Head conspicuously produced beyond eyes; eyes distant
 from fore margin of head.....**Organothrips** Hood.
 Eyes anterior, their fore margins about on a level with
 anterior edge of front of head.....**Leucothrips** Reuter.
- 7(5). Antennae seven-segmented 8
 Antennae eight-segmented 9
- 8(7). Postero-lateral angles of prothorax with three prominent
 bristles**Docidothrips** Priesner.
 Postero-lateral angles of prothorax with two prominent
 bristles 10
- 9(7). Antennal sense trichomes simple.....**Bregmatothrips** Hood.
 Antennal sense trichomes forked.....
**Taeniothrips** Amyot and Serville.
- 10(8). Anterior ocellus placed anterior to fore margins of eyes;
 fourth antennal segment elongate; ovipositor reduced;
 males with a pair of heavily sclerotized, finger-like proc-
 esses on posterior margin of ninth abdominal tergite..
**Plesiothrips** Hood.
 Not so**Thrips** Linnaeus.

Genus **MEROTHRIPS** Hood, 1912:132

Two species of this genus have been recorded in our literature. However, there is some reason to believe that only one species is involved. *Mercothrips morgani* is the name assigned to a form whose colonies have been found to consist entirely of wingless individuals both in Hawaii and in North America. Our *Mercothrips hawaiiensis*, however, is known only from winged forms. It is of interest that the only known specimens of *Mercothrips hawaiiensis* were taken in a wind trap placed in a warm, lowland pineapple field, but that the *Mercothrips morgani* colonies thus far found in Hawaii have been taken in cool, high, mountain localities.

Mercothrips hawaiiensis Moulton (fig. 216, e).

Mercothrips hawaiiensis Moulton, 1937:411.

Molokai(type locality).

Immigrant, but as yet known only from the Hawaiian Islands; possibly the same as the following species.

Hostplant: unknown (the type series was taken in a wind trap).

Mercothrips morgani Hood.

Mercothrips morgani Hood, 1912:132, pl. 5, figs. 1-3.

Hawaii.

Immigrant. A North American species described from Illinois and Kentucky. First reported from Hawaii by Bianchi (1946:513) from specimens collected in Hawaii National Park by C. J. Davis.

Hostplants: *Heimerliodendron brunonianum*, *Perottetia sandwicensis*, *Pittosporum confertiflorum*, *Santalum paniculatum*, *Urera sandwicensis*.

Genus **SELENOTHRIPS** (Karny)

Heliothrips, subgenus *Selenothrips* Karny, 1911.

Selenothrips rubrocinctus (Giard) (fig. 220, d).

Physopus rubrocinctus Giard, 1901:264.

Heliothrips rubrocincta (Giard) Franklin, 1908:719-723, pl. 64, figs. 10, 14; pl. 65, figs. 17, 20, 21, with detailed redescription.

Bagnall, 1910:699.

The red-banded thrips.

Kauai. Oahu. Molokai, Maui, Hawaii.

Immigrant. A widespread species. First recorded from the Hawaiian Islands by Bagnall (1910:699).

Hostplants: azalea, croton, *Eugenia cumini* (Java plum), guava, *Litchi*, mango, *Passiflora* (passion fruit), *Schinus terebinthifolius* (Christmas berry). A pest in the West Indies.

This species may at times cause considerable damage by causing cracking or silvering of leaves and fruits. Mango fruits may become excessively spotted with the dried excrement of this species, which is clear when dropped but dries to dark-brown blotches. The clear globules, when deposited, may measure 0.5 mm. across, but may dry to over a millimeter in extent, and many hundreds may be present on a single fruit. Moreover, the fruits are sometimes severely damaged by extensive feeding and oviposition. The skin becomes discolored, cracks, wrinkles and shrivels as though dried and sunburned, and the flesh may become flabby beneath the wrinkled skin areas.

The larvae are conspicuously colored. They are basically yellowish with the abdomen bright red across the two basal segments, with most of the other segments tinged with orange. The penultimate abdominal segment is apically tinged with black, and the caudal segment is conspicuously dark brown or black and is armed with six very long, conspicuous, radiating, dark setae. The adults are dark brown with dusky wings, pale feet and bicolored antennae. In life, these insects usually carry the tip of the abdomen curved up over the thorax and are very striking when seen walking about on the host, especially when they have a large globule of excrement held in the "basket" formed by the large, radiating, caudal setae of the brightly colored larvae. They pupate on the host.

Genus **SCOLOTHRIPS** Hinds, 1902:157

This genus contains three species, the best known of which is the following:

Scolothrips sexmaculatus (Pergande) (fig. 222, a).

Thrips 6-maculata Pergande, 1892:539.

Thrips pallida Beach, 1896:226.

Scolothrips sexmaculatus (Pergande) Hinds, 1902:157, pl. 4, figs. 42, 45, re-description. Genotype.

Bailey, 1939:43-47, fig. 1, bionomics.

Kauai, Oahu, Hawaii.

Immigrant. Cosmopolitan. First recorded from Hawaii by Bagnall (1910:700) from specimens collected by Fullaway in Honolulu.

Hosts: a predaceous species; feeds on the eggs, young and adults of "red spiders" and other mites. Found on *Psidium*, beans, *Thunbergia grandiflora*, *Xanthium canadense* and on a large number of other plants in Hawaii when they are mite-infested.

This species varies in color from whitish to pale yellow to orange-yellow and has three dark maculae on each fore wing. The mature larvae and pupae are similarly colored. The entire life cycle is passed on the hostplant. The following notes were obtained from Bailey (1939:43-47). Bisexual reproduction appears to be usual. The females lay only about four to six eggs which hatch after six to ten days; the larval stage lasts five days or longer, depending upon food and temperature; the prepupal stage lasts a single day, and the pupal stage about five days; the adults live from two to three weeks.

A most confusing situation exists concerning the original description of this species. Many authors cite the original description as *Trans. St. Louis Acad. Science*, 5:542, 1894. The 1894 volume is 7, not 5, and no paper by Pergande nor a *Thrips 6-maculata* is described in that volume. However, the original description appears as a footnote to a paper by Duffey on Carabidae, Coccinellidae and red spiders in the journal cited, volume 5, published in 1892!

Genus **FRANKLINIELLA** Karny, 1910

KEY TO THE SPECIES OF FRANKLINIELLA LISTED FROM HAWAII

1. Dark-colored species **fusca** (Hinds).
Pale species 2
2. Setae mostly hyaline **williamsi** Hood.
Setae brownish **sulphurea** Schmutz.

Frankliniella fusca (Hinds).

Euthrips fuscus Hinds, 1902:154, pl. 4, figs. 40, 41.

Hawaii.

Immigrant. Described from Massachusetts. First found in the Hawaiian Islands by William Look at Hilo in 1945.

Hostplant: narcissus (bulbs).

Frankliniella sulphurea Schmutz.

Frankliniella sulphurea Schmutz, Sitz Ber. Akad. Will. Wien 123:1019, 1913
(I have not seen this reference).

Karny, 1926:195, pl. 17, fig. 2; 1928:255, fig. 2a.

Oahu, Hawaii.

Immigrant. Perhaps an Oriental species; common in India. First discovered by Pemberton and Holdaway at Poamoho, Oahu, in 1942. (See Proc. Hawaiian Ent. Soc. 11[3]:273, 1943, under *F. occidentalis*.)

Hostplants: flowers of bush and lima beans, eggplant, hibiscus, lantana, monkey-pod, okra, orchids, tomato.

Frankliniella williamsi Hood.

Frankliniella williamsi Hood, 1915:19, pl. 2, figs. 4, 5.

Frankliniella flavens Moulton, 1928:108 (described from Honolulu).

Kauai, Oahu.

Immigrant. Described from North America (type locality: Washington, D. C.). F. A. Bianchi tells me that it has been intercepted at Honolulu on green corn from California. First recorded from the Hawaiian Islands by Moulton, 1928:108.

Hostplants: corn, *Panicum purpurascens*, *Sorghum vulgare*.

This species, essentially a grass thrips having a narrow host range, is always found in large numbers on corn, a preferred host, wherever it grows.... This thrips breeds freely in the folds of rolled heart leaves of young plants as well as in the interspace, usually at the basal portion of the ear, between the overlapping husks of the young or mature ears.... It appears that moist surroundings, such as wet areas near the lower forests and well-irrigated or damp areas of the open lowlands, are the preferred habitat and that increase in populations occurs in the winter months. (Sakimura, in Sakimura and Krauss, 1945:321-322.)

Genus **ORGANOTHRIPS** Hood, 1940:423**Organothrips bianchii** Hood (fig. 221, a-e).

Organothrips bianchii Hood, 1940:423, pl. 24. Genotype.

The taro thrips.

Kauai, Oahu (type locality: Kailua), Molokai, Hawaii.

Immigrant, but not yet recorded elsewhere. Probably a western Pacific species.

Hostplant: taro (*Colocasia*) (irrigated types).

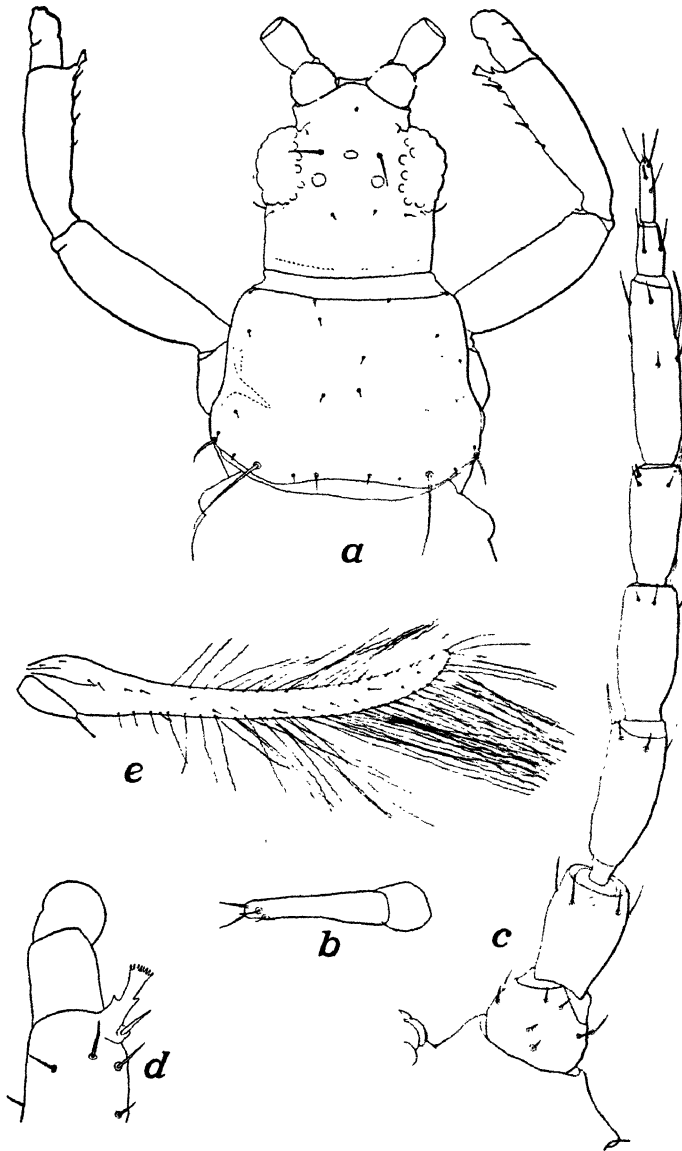


Figure 221—*Organothrips bianchii* Hood. a, head and prothorax, holotype female (all antennal setae, and most of those on legs omitted); b, left maxillary palpus, paratype female; c, left antenna, paratype female; d, left fore tarsus and tip of tibia, paratype female (tarsal setae omitted); e, right fore wing, paratype female. (After Hood, 1940.)

1. Body predominantly pale; wings uniformly dark..... **xanthius** (Williams).
 **cyperaceae** Bianchi.
 Body pale; wings pale **cyperaceae** Bianchi.
 Body predominantly dark brown; wings either pale or dark... 2

- 2(1). Fore wing with about six distal spines on fore vein.....
**simplex** (Morison).
 Fore wing with about three distal spines on fore vein..... 3
- 3(2). Wings pale**alliorum** Priesner.
 Wings predominantly dark 4
- 4(3). Interocellar spines within ocellar triangle, on a line between
 anterior margins of posterior ocelli.....**gracilis** Moulton.
 Interocellar spines on or outside of ocellar triangle, anterior
 to a line drawn between fore edges of posterior ocelli..... 5
- 5(4). Antennal segments three to five entirely pale; interocellar
 spines long, on ocellar triangle; anterior ocellus distant
 from posterior ocelli, all ocelli widely separated.....
**frici** (Uzel).
 Antennal segment three pale, four and five dark distad;
 interocellar spines short, outside triangle; ocelli closely
 grouped, anterior ocellus very close to posterior ocelli
**hawaiiensis** (Morgan).

Taeniothrips alliorum Priesner.

Taeniothrips alliorum Priesner, 1935:128.

Taeniothrips carteri Moulton, 1936:183 (type locality: Kilauea, Kauai): syn-
 onymy by Moulton, 1937:410.

Kauai, Oahu, Molokai, Maui, Lanai, Hawaii.

Immigrant. Widespread; described from Formosa. First recorded from the
 Hawaiian Islands (as *carteri*) by Moulton (1936:183) from specimens collected
 on Kauai by Carter.

Hostplants: onion (common), *Emilia sonchifolia*.

Taeniothrips cyperaceae Bianchi (fig. 223, D, E).

Taeniothrips cyperaceae Bianchi, 1945:283, pl. 17, figs. D, E.

Oahu (type locality: Honolulu), Hawaii.

Immigrant. First found in the Hawaiian Islands in 1940, but not known else-
 where.

Hostplants: *Cyperus rotundus* (nutgrass), *Solanum nigrum*, *Vinca major*.

Only females have been found. It resembles *Taeniothrips leptosperon* Moulton
 from New Guinea.

Taeniothrips frici (Uzel).

Physopus frici Uzel, 1895:126.

Priesner, 1928:288, pl. 4, fig. 61.

Maui, Hawaii.

Immigrant. Widespread. First recorded from Hawaii by Moulton (1937:410) from specimens collected at Olinda, Maui, in 1933 by Linford.

Hostplants: *Acacia koa*, dandelion (*Taraxacum officinale*), *Hypochaeris radicata*, *Styphelia tameiameia*; a flower feeder.

Taeniothrips gracilis Moulton.

Taeniothrips gracilis Moulton, 1928: 289, pl. 5, fig. 1.

Oahu, Molokai, Hawaii.

Immigrant. Described from Japan and Formosa. First recorded from the Hawaiian Islands by Moulton (1937:410) from specimens collected in 1930 by Sakimura.

Hostplants: *Hymenocallis declinata*; usually a flower feeder, but Bianchi has found it feeding on stems and leaves of *Crinum* and discoloring the plant.

Taeniothrips hawaiiensis (Morgan).

Euthrips hawaiiensis Morgan, 1913:3, figs. 5-8.

Thrips albipes Bagnall, 1914:25; synonymy by Steinweden, 1933:286.

Thrips hawaiiensis forma *imitator* Priesner, 1934:267.

Moulton, 1928:110, describes the male. Steinweden (1933:286) suggests that *Physothrips pallipes* Bagnall (1916:397) may also be a synonym. Bianchi has told me that he believes that *Thrips alcuritis* Moulton (1933:29, fig. 1) from Tahiti and *Thrips leucaenae* Moulton (1942:9) from Guam may be synonyms.

The Hawaiian thrips.

Kauai, Oahu (type locality: Honolulu), Molokai, Maui, Hawaii, Midway.

Immigrant. A widespread Oriental species.

Hostplants: This species is a widespread flower feeder which lives in large colonies, and it has been recorded from many families of plants, but mostly from Leguminosae and Convolvulaceae from seashore to mountain tops. It is said to be a minor pest of garden beans, and has been reported to damage orchids. *Acacia confusa*, *Acacia farnesiana*, *Acacia koa*, *Aleurites moluccana*, alfalfa, asparagus, *Astelia menziesiana*, aster, *Argemone alba* var. *glauca* (prickly poppy), avocado, *Batis maritima*, bean, bell pepper, *Buddleia japonica*, bush bean, *Calotropis gigantea* (crown flower), canna, *Cassia leschenaultiana* (misidentified as *mimosoides*), *Cattleya*, *Commelina diffusa* (nudiflora), *Coronopus didymus* (*Senebiera didyma*), cotton, *Crinum*, *Crotalaria juncea*, *Crotalaria mucronata* (saltiana), *Datura stramonium*, *Delonix regia*, *Dendrobium*, *Dioclea violacea* ("maunaloa"), *Dombeya spectabilis*, Easter lily, *Gladiolus*, guava, *Hemerocallis flava*, *Hippobroma longiflora* (Star of Bethlehem), Hubbard squash, *Hydrangea*, *Hypochaeris radicata*, *Ipomoea cairica* (tuberculata), *Ipomoea cairica* var. *lineariloba*, *Ipomoea congesta* (indica and *insularis* in Hawaiian literature), *Ipomoea pes-caprae*, *Lantana*, *Leucaena glauca*, *Macaranga*, *Melaleuca leucadendron*, *Mirabilis jalapa*, monkeypod, native and cultivated *Hibiscus* (occasionally abundant on flowers), *Operculina aegyptia* (*Ipomoea pentaphylla*), orchids, *Pandanus*, pole bean, *Prosopis*, radish, *Rosa*, *Rubus penetrans*,

Scaevola frutescens, soy bean, *Spathodea campanulata*, squash, *Styphelia*, *Telosma cordata*, *Tithonia diversifolia* (*rotundiflora*), *Tricholaena repens* (*rosea*), *Tritonia crocosmaeflora* (*potsii*), *Vanda*, *Verbesina encelioides*, *Vitex trifolia* var. *simplicifolia* ("polinalina"), *Waltheria americana*, *Wikstroemia*, *Yucca*.

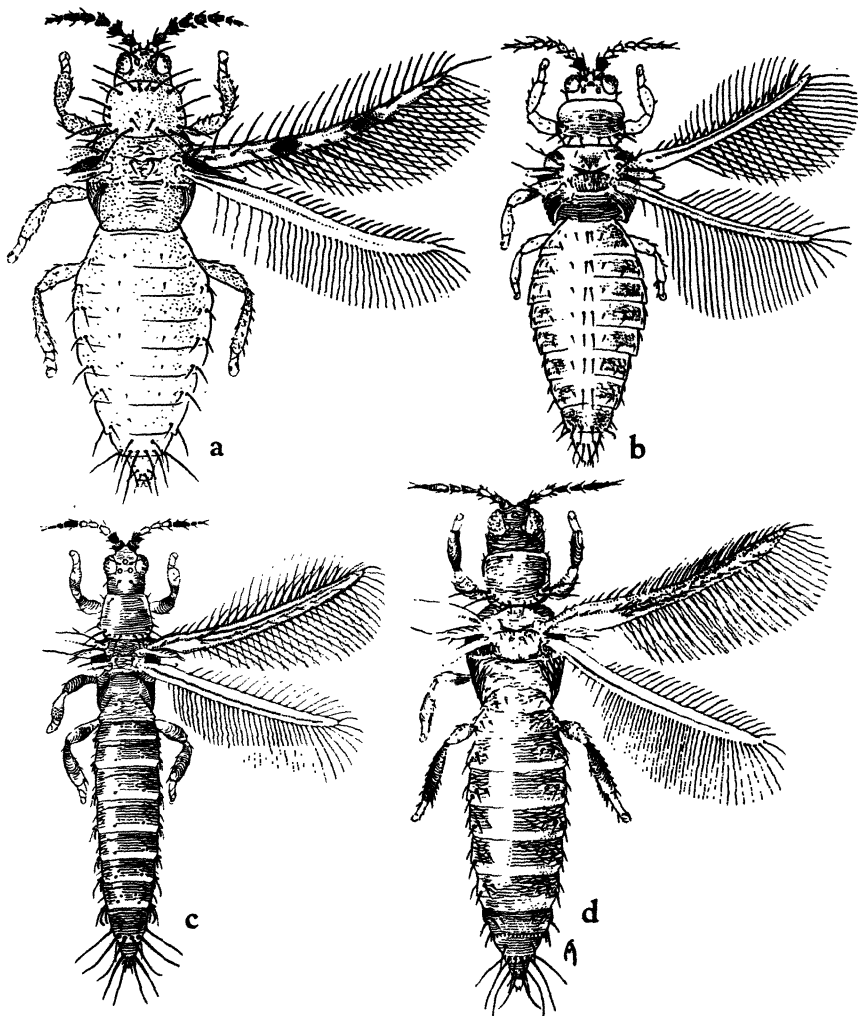


Figure 222—*a*, *Scolothrips sexmaculatus* (Pergande); *b*, *Leucothrips piercei* (Morgan); *c*, *Bregmatothrips venustus* Hood; *d*, *Taeniothrips simplex* (Morison). (Abernathy drawings; not to same scale.)

Control: tartar emetic sprays have been used with success in controlling this thrips on orchids.

This is a confusing species. One of the principal characters used to separate *Taeniothrips* from *Thrips* is whether the antennae are seven-segmented (*Thrips*) or eight-segmented (*Taeniothrips*). Yet, one may find both seven- and eight-segmented individuals of this species in the same colony. Moreover, some specimens have one antenna seven-segmented, the other eight-segmented. Specimens with only six antennal segments are seen occasionally, as are other irregularities. Sakimura (Sakimura and Krauss, 1944:117) found 91 out of 107 individuals examined to have eight-segmented antennae (the form *imitator* of Priesner). No colonies have been seen in which all the individuals had the same number of antennal segments. I have, therefore, placed this species in the key to *Thrips* as well as in *Taeniothrips*. It is frequently taken in company with *Thrips tabaci*. Takahashi (1936) reported that this species is the most dominant and polyphagous thrips in Formosa.

Taeniothrips simplex (Morison) (fig. 222, d).

Physopus simplex Morison, 1930:12.

Taeniothrips gladioli Moulton and Steinweden, 1931:20, fig. 1. Synonymy by Moulton, 1936:184.

The gladiolus thrips.

Kauai, Oahu, Maui, Hawaii.

Immigrant. Widespread. First discovered in Hawaii by Chock in 1932 in Honolulu.

Hostplants: a pest of *Gladiolus*, *Tritonia crocosmaeflora*.

When this pest first appeared in Hawaii, it spread rapidly, caused great damage, forced some gladiolus growers out of business and caused some amateur breeders to give up gladiolus growing. However, the severity of attack has dwindled greatly, and we do not have many complaints of heavy damage done by it now.

The attacks of this species cause bleaching or silvering of the leaves, the flowers fail to develop properly and become streaked and bleached, normal growth is inhibited, new corms are not developed and heavy infestation of corms causes them to shrivel and fail to germinate. The thrips continue feeding on stored corms.

McKenzie (1935:4) found that in the summer in California the length of the life cycle was from 14 to 19 days. The females can reproduce parthenogenetically, but without mating give rise only to males. A single female may lay between 100 and 200 eggs over a period of one to two and one-half months. The white eggs take five to six days to hatch; the first-stage larvae are translucent white with red eyes and develop in two to three days; the second-stage larvae are pale yellow and last two to four days; the prepupa is orange and lasts two to three days; the pupa, which lasts three days, is at first orange, but soon turns to yellow with large red eyes and its wing pads extend to abdominal segments seven or eight. "The adult . . .

is dark-brown to black with the head and thorax usually darker than the abdomen. The wings have a light-colored area at the base where they join with the thorax and when folded give the appearance of a band across the insect." (McKenzie, 1935:4.)

Parasite: *Thripoctenus russelli* Crawford (Hymenoptera: Eulophidae).

Control: McKenzie (1935) recommends a spray consisting of manganese arsenate, $\frac{1}{4}$ pound; brown sugar, $4\frac{1}{8}$ pounds; and water, $6\frac{1}{4}$ gallons (or, for large quantities, 4 pounds, 66 pounds, and 100 gallons of water, respectively). "In order to insure clean flowers and to prevent rapid increase in population of the thrips, it is necessary to begin spraying when the plants are about 2 inches high." (McKenzie.) Spraying should be done once a week. More recent studies have shown that a spray made from two pounds tartar emetic and four pounds brown sugar in 100 gallons of water is an effective spray, and it has been widely adopted. Another good spray is one quart of 40 percent nicotine sulphate and three gallons of corn syrup to 100 gallons of water. For control on the stored corms, naphthalene flakes are effective and easy to use. Use an ounce to each 100 corms placed in a tightly closed paper bag for at least three weeks. Corrosive sublimate mixed one ounce to seven gallons of water kills all stages on unpeeled corms dipped for 17 hours.

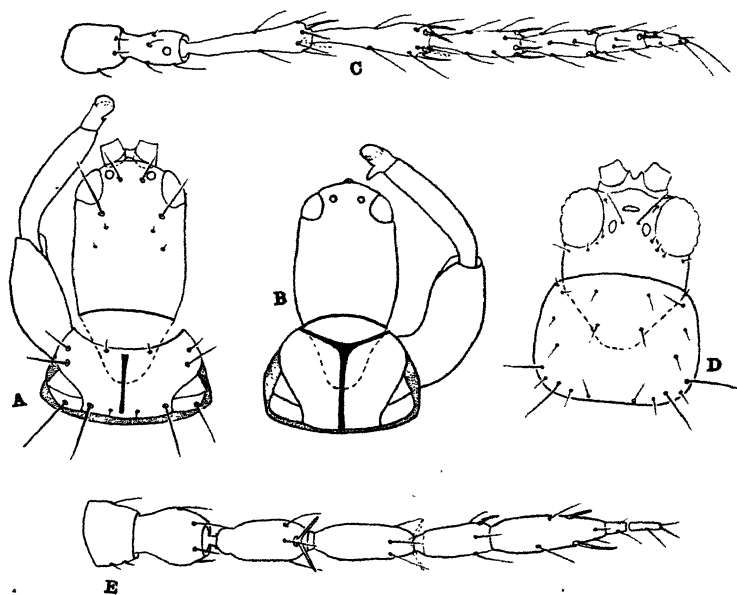


Figure 223—Details of some thrips: A, *Rhaebothrips major* Bagnall, macropterous female; B, the same, macropterous male, all setae omitted; C, the same, left antenna of female, dorsal view; D, *Taeniothrips cyperaceae* Bianchi, macropterous female; E, left antennae of same, dorsal view with some minor setae omitted. (After Bianchi, 1945.)

Taeniothrips xanthius (Williams).

Physothrips xanthius C. B. Williams, 1917:59, fig. 1.

Oahu.

Immigrant. Described from Trinidad, British West Indies. First found in Hawaii by Swezey in 1935 at Honolulu.

Hostplants: orchid, *Cypripedium*, *Cattleya*, *Asystasia gangetica*.

Control: nicotine sulphate diluted 1:400 to 600 has been recommended for use on orchids.

"The larvae and pupae are found with the adults on the upper surfaces of the leaves [of *Cattleya* orchids], particularly near the mid rib and toward the base of the leaf. They cause injury by piercing the surface, resulting in brownish spots or patches on the leaves. In severe cases the plant may be entirely killed." (C. B. Williams, 1917:61.)

Sakimura (Proc. Hawaiian Ent. Soc. 12 [1]:26, 1944) recommends keeping orchid houses free from the alternate host *Asystasia gangetica* as essential to the control of this pest. It is our worst thrips pest of orchids.

Genus **PlesiOTHrips** Hood, 1915:129

PlesiOTHrips panicus (Moulton).

Thrips panicus Moulton, 1929:61.

PlesiOTHrips panicus (Moulton) Hood, 1936:258.

Kauai, Oahu, Molokai (type locality).

Immigrant. Widespread. First recorded from the Hawaiian Islands by Moulton, 1929:61. The type series consisted of specimens from sugarcane from Hawaii and *Panicum maximum* from Cuba.

Hostplants: *Cenchrus echinatus*, *Digitaria sanguinalis* (*Syntherisma sanguinalis*), *Echinochloa crus-galli*, *Echinochloa crus-garonis*, *Eleusine indica*, *Emilia sonchifolia*, *Pandanus* (male flowers), *Paspalum conjugatum*, *Paspalum dilatatum*, pineapple, rice, *Sctaria geniculata*, sugarcane, *Trichachne insularis* (*I'alota insularis*).

Hood (1936:258) says that this species is "closely allied to, if not identical with, *P. perplexus* (Beach)," the genotype, which is figured by Hood, 1915:129.

Genus **THRIPS** Linnaeus, 1758:457

This is a large, complex group which is largely in a taxonomic muddle.

KEY TO THE SPECIES OF THRIPS FOUND IN HAWAII

(Excepting *Thrips multispinus* Bagnall, which I have not seen.)

1. Caudal margins of abdominal tergites one to eight serrate (difficult to see on some specimens): on Compositae (subgenus *Microcephalothrips*)... **abdominalis** (Crawford).
At most only hind margins of seventh and eighth abdominal tergites serrate 2

- 2(1). Fore wings yellow, but with a brown band at middle and at apex (part of subgenus *Isoneurothrips*)..... **fasciatus** (Moulton).
Fore wings not banded 3
- 3(2). Ocellar crescents gray or olive colored (Note: in cleared specimens it will not be possible to tell the color; proceed to part 4)..... **tabaci** Lindeman.
Ocellar crescents orange or reddish..... 4
- 4(3). Fore wing with anterior vein closely, unusually evenly set with numerous stout spines beyond middle, the spines often evenly placed from near base to apex (subgenus *Isoneurothrips*) 5
Fore wing with anterior vein with only a few irregularly placed stout spines beyond middle (subgenus *Thrips*) 10
- 5(4). Predominantly dark-brown species 6
Pale yellowish or brownish-yellow species..... 7
- 6(5). Antennae comparatively long and slender, length about 300 microns **antennatus** (Moulton).
Antennae comparatively short and stout, length about 225 microns **fullawayi** (Moulton).
- 7(5). Antennae with four basal segments pale, the others brownish **dubautiae** (Moulton).
Antennae with only the basal first or first and second segments pale 8
- 8(7). Antennae with first two segments pale.... **carteri** (Moulton).
Antennae with only first segment pale..... 9
- 9(8). Fore wing with about 38 costal spines; caudal abdominal segment dark brown in female..... **australis** Bagnall.
Fore wing with about 28 costal spines; caudal abdominal segment concolorous with remainder of abdomen in female **williamsi** (Moulton).
- 10(4). Predominantly yellowish species 11
Predominantly brown species 12
- 11(10). Body spines long, stout, dark brown; antennal segments three to seven dark brown, two pale brown; interocellar spines strongly developed and conspicuous..... **nigropilosus** Uzel.
Body spines short, pale brown; antennal segments three to seven pale brown, two dark brown; interocellar spines minute and inconspicuous..... **tabaci** Lindeman.
- 12(10). Legs dark brown..... **trehernei** Priesner.
Legs pale 13
- 13(12). Antennal segments three and four pale; antecellar spines strongly developed, longer than interocellar spines.... **saccharoni** Moulton.
Antennal segment three only pale; antecellar spines inconspicuous, much shorter than interocellar spines [Note: if your specimen runs to here, it may be *Taeniothrips hawaiiensis* (there is no *Thrips hawaiiensis*) which is a variable and confusing species. See discussion under *Taeniothrips*] **Taeniothrips hawaiiensis** (Morgan).

Subgenus **Microcephalothrips** (Bagnall, 1926:113, as a genus) Priesner, 1928:442

Thrips (Microcephalothrips) abdominalis (Crawford) (fig. 226, a).

Thrips abdominalis Crawford, 1910:157, fig. 65.

Microcephalothrips abdominalis (Crawford) Bagnall, 1926:114. Genotype of *Microcephalothrips*.

See Bailey, 1937:121, for discussion, illustrations and detailed synonymy.

The composite thrips.

Kauai, Oahu, Maui, Hawaii.

Immigrant. Nearly cosmopolitan. First recorded from the Hawaiian Islands by Moulton (1928:110) from specimens collected by Swezey at Honolulu in 1926 and 1927.

Hostplants: aster, *Bidens pilosa*, *Chrysanthemum*, *Emilia coccinea*, *Emilia sonchifolia*, *Erigeron*, *Gaillardia pulchella*, *Ipomoea congesta* (indica), *Ipomoea pes-caprae*, *Lantana*, *Malva*, *Tithonia diversifolia*, *Verbesina encelioides*.

This is a variable species which may be macropterous or brachypterous. The entire life cycle is passed in the flower heads. Bailey (1937:125) reports that "The eggs are inserted in the more tender portions of the flower parts, stems and buds. The length of the egg stage was not definitely determined but is probably in the neighborhood of five days. During the early fall [in California] the larval stage extends over a period of two weeks. The prepupal stage lasted one to two days and the so-called pupal stage two to three days. The pupae are found unprotected in the flower heads only, in company with all other stages." He noted that the predaceous bug *Orius tristicolor* White fed on this species in California.

Subgenus **Thrips** (Linnaeus, 1758)

Thrips (Thrips) nigropilosus Uzel.

Thrips nigropilosus Uzel, 1895:198, pl. 6, figs. 105-106.

Priesner, 1928:409.

The chrysanthemum thrips.

Kauai, Oahu, Maui, Hawaii.

Immigrant. Cosmopolitan. First recorded from the Hawaiian Islands by Moulton (1937:410) from specimens collected by Sakimura at Kapahulu, Oahu, in 1936.

Hostplants: aster (injury to seedlings), *Arctium lappa* (burdock), carrot, celery, *Chrysanthemum*, *Datura stramonium*, eggplant, *Emilia sonchifolia*, *Hypochaeris radicata*, lettuce (damage done; the most important thrips on this host in Hawaii), *Plantago lanceolata*, potato, spinach.

Control: nicotine sulphate, derris extract sprays and sulphur dusting have been used successfully.

Thrips (Thrips) saccharoni Moulton (figs. 225; 226, d).

Thrips saccharoni Moulton, 1928:111, pl. 1, fig. 1.

The sugarcane thrips.

Kauai, Oahu (type locality: Honolulu), Molokai, Hawaii.

Immigrant. Tropicopolitan.

Hostplants: corn, *Panicum purpurascens* (*barbinode*), sugarcane.

"It often fairly swarms in and about the central leaf-roll of the sugarcane plant and is quite active, and when exposed may jump and fly away." (F. X. Williams, 1931:94.) When abundant, it may cause mottling of the leaves.

Sakimura (Sakimura and Krauss, 1945:322) reports that perhaps wetland and dryland phases occur which differ in coloration. Sometimes both "forms" are found together on the same plant.

Thrips (Thrips) tabaci Lindeman (figs. 224; 226, c).

Thrips tabaci Lindeman, 1888:15, 61-75.

For detailed synonymy, see Priesner, 1928:433, and Hinds, 1902:179-184; for description, notes and illustrations, Speyer, 1934; for bionomics in Hawaii, see Sakimura, 1932:884-891.

The onion thrips.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii, Midway, Kure (Ocean).

Immigrant. Cosmopolitan. First recorded in the Hawaiian Islands by Fullaway in 1915.

Hostplants: *Acacia farnesiana*, *Acacia koa*, *Acanthospermum australe* (*xanthoides*), *Ageratum conyzoides*, alfalfa, *Amaranthus viridis* (*gracilis*), *Amaranthus retroflexus*, *Anthurium*, bell pepper, *Bidens pilosa*, *Bothriospermum tenellum*, *Brassica chinensis*, *Brassica nigra*, broad bean, broccoli, cabbage, *Callistephus chinensis* (Chinese aster), carnation, carrot, *Cassia leschenaultiana* (misidentified as *mimosoides*), *Cassia occidentalis*, *Cassia tora*, cauliflower, celery, *Cenchrus*, *Centella asiatica* (*Hydrocotyle asiatica*), chard, chicory, *Coronopus didymus* (*Senebiera didyma*), *Crotalaria juncea*, *Crotalaria mucronata* (*saltiana*), *Crotalaria spectabilis*, *Cucumis dipsaceus*, *Cuphea carthagenensis* (misidentified as *hyssopifolia*), *Digitaria violascens* (*Syntherisma chinensis*), *Digitaria sanguinalis*, *Datura stramonium*, edible-pod pea (*Pisum sativum*), eggplant, *Eleusine indica*, *Emilia coccinea*, *Emilia sonchifolia* (*sagittata*), endive, *Erechtites hieracifolia*, *Erigeron albidus*, *Erigeron canadensis*, *Euphorbia hirta*, *Franseria strigulosa* (*Ambrosia artemisiaefolia*), *Gnaphalium luteo-album*, *Ipomoea congesta*, *Ipomoea cairica* (*tuberculata*), kohlrabi, *Lantana camara*, lettuce, *Leucaena glauca*, *Lupinus*, *Malva*, *Mimosa pudica*, *Mirabilis jalapa*, nasturtium, New Zealand spinach, *Nicandra physalis*, *Nicotiana*

glutinosa, *Nothopanax guilfoylei*, onion (a preferred host), *Oxalis martiana*, papaya, parsley, *Paspalum conjugatum*, *Phaseolus lathyroides*, *Phytolacca acinosa*, pigeon pea, pineapple, *Pluchea indica*, *Portulaca oleracea*, potato, *Prosopis chilensis* (*juliflora*), radish, *Richardia scabra* (*Richardsonia scabra*), rose, *Solanum nodiflorum*, *Sonchus oleraceus*, soy bean, *Stachys arvensis*, *Stachytarpheta cayennensis* (*dichotoma*), stocks, *Tithonia rotundifolia*, tobacco, tomato, *Tricholaena repens*, *Verbena litoralis* (misidentified as *V. bonariensis*), *Vernonia cinerea*, *Vigna sinensis*, *Waltheria americana*, white radish, *Yucca*.

Parasites: *Thripoctenus brui* Vuillet, *Thripoctenus russelli* Crawford (Hymenoptera: Eulophidae).

Predators: *Aeolothrips fasciatus* (Linnaeus), *Scolothrips sexmaculatus* (Perge) (predaceous thrips).

This species causes concern to the growers of pineapples and many truck crops in the islands, and it is a transmitter of yellow-spot virus. The wide host range of the species makes it difficult to control. It is the most important of all the thrips pests.

Reproduction in this species in Hawaii is mostly by parthenogenesis. Only five out of 5,000 specimens examined by Sakimura (1932:887) were found to be males. In Hawaii the average length of life cycle and stages has been found by Sakimura (1932:890) to be as follows: egg, 4.5 days; first instar, 4.6; second instar, 4.6; prepupal, 1.5; pupal, 3.3; life cycle, 18.5; preoviposition period, 6; duration of oviposition, 22.5; postoviposition period, 4; average number of eggs deposited by unmated females, 37.4. Large populations develop quickly under Hawaiian conditions.

The feeding scars on *Emilia sonchifolia* (*sagittata*) are described by Sakimura (1932:886) as follows: "the silvery whitish sunken area is the direct result of their attack. Young terminal leaves frequently show malformations when heavily attacked, with crinkly surfaces, sunken and raised thin areas, marginal erosion, margin curling inwardly and a chlorotic yellowish appearance with grayish color along all the large veins. These injuries are produced by both viruliferous and non-viruliferous insects. The malformed leaves appear in bunchy form on terminals."

Because of the importance of this pest in the transmission of pineapple yellow-spot virus, the Pineapple Research Institute of Honolulu imported the internal parasite *Thripoctenus brui* Vuillet from Japan in 1932-1934 to aid in its control (see Sakimura, 1937:799). Considerable research concerning virus transmission by this species has been conducted by members of the Pineapple Research Institute (see bibliography). The virus attacks a number of wild hostplants, among which is *Emilia sonchifolia* (*sagittata*), a common, widespread weed and a favorite host of the thrips.

Sakimura (1940:281) presented new data and reviewed the old evidence to show that pineapple yellow-spot is the same as tomato spotted-wilt, which attracted notice in Hawaii in 1937 and has since caused considerable trouble in the islands. Pineapple yellow-spot was first noticed in Hawaii in 1926. This disease is carried

by *Thrips tabaci* to a number of other plants, including *Emilia* species, spinach, broad bean, celery, potato, eggplant, bell pepper, tobacco, *Nicotiana glutinosa*, *Datura stramonium*, *Petunia*, chicory, endive and lettuce; but beet, Swiss chard, cabbage, cauliflower, New Zealand spinach, *Commelina diffusa*, *Commelina benghalensis* and summer *Chrysanthemum* are not susceptible, according to Sakimura (1940: 297). Tomato plantings sometimes suffer extensive damage as a result of the disease.

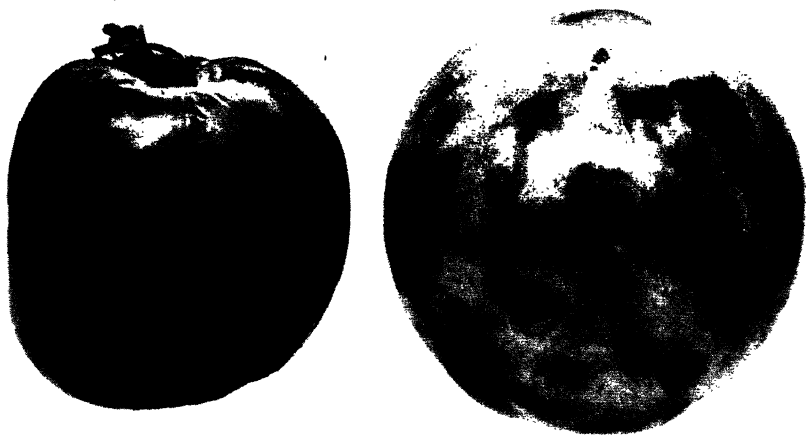


Figure 224—Tomato fruits showing symptoms of yellow spotted-wilt of tomatoes which is transmitted by *Thrips tabaci* Lindeman. (Photograph by K. Sakimura, Pineapple Research Institute.)

Linford (1932:301–324) noted that although yellow-spot is one of the major diseases of pineapple in Hawaii and may kill the plants (but see note below by Sakimura), “The pineapple plant, even as a young seedling, appears relatively unfavorable for the growth and reproduction of *Thrips tabaci*...” (p. 312). He found the incubation period for the virus in the *Thrips* to be about 10 days, and in *Emilia sonchifolia* (*sagittata*) it is about 15 days (mean) and in pineapple, 12 days (mean). Adult thrips raised from larvae on non-infected plants cannot transmit the disease, even if they feed, as adults, on infected plants, but adults reared from larvae raised on infected plants can transmit the disease to a healthy plant.

Carter (1939:275) said,

It is evident...that a considerable reservoir of virus may exist in the pineapple fields with little or no transfer to pineapple plants taking place. This is readily explainable on the difference in suitability of the two plants as thrips hosts. A few scattered wind-blown thrips would be sufficient to infest and infect the relatively small populations of *Emilia* present. Infestation of pineapple plants, however, does not occur except rarely and even then only for a short period during blossoming, the thrips' sojourn on pineapple being transient. This transient stage is sufficient to infest the pineapple if the insect is viruliferous and the plant susceptible. There is no evidence to indicate movement of thrips from pineapple to pineapple,

nor is movement from undisturbed *Emilia* growing among pineapple to nearby pineapple plants likely. There is, furthermore, no correlation between *Thrips tabaci* populations on *Emilia* in the sampled areas and disease in nearby pineapple fields, probably for the same reason, that undisturbed *Emilia* is a favoured host from which movement does not normally occur.

Sakimura (1947:85) says, however, that "with the exception of some minor localized outbreaks here and there, this disease has rarely proved to be serious" to pineapples.

Occasionally, the young leaves of papaya are deformed by attacks of this species. Onions are severely attacked in dry areas or at times of drought. It is a minor pest of garden beans and occasionally causes damage to cabbage.

Control: Carter (1932:1031) reported that tobacco dust was the most effective insecticide used in the control of yellow-spot on pineapples. Other workers have used nicotine sulphate successfully for control on onions and asparagus which have been damaged in the islands. Overhead irrigation or spraying with water is a simple and effective control practice where possible. The use of tartar emetic-sugar-water (2-4-100 parts) spray has been found to be successful for control on onions in some places on the mainland. The spray is applied five or six times at about weekly intervals when the onions reach a height of four to six inches.

Sakimura has told me that he has noted that the rainy-season, winter form of this species is darker in color in Hawaii than the summer form.

***Thrips (Thrips) trehernei* Priesner.**

Thrips trehernei Priesner, 1928:356, footnote.

Oahu.

Immigrant. Widespread. This species was recorded from Hawaii for the first time by Moulton (1936:184) from a single example taken from a pineapple at Honolulu in 1930 by Ito.

Hostplant: pineapple (?).

Subgenus *Iseurothrips* (Bagnall, 1915)

In addition to the following species, other new forms are known to occur here.

***Thrips (Iseurothrips) antennatus* (Moulton).**

Iseurothrips antennatus Moulton, 1928:112.

Endemic (?). Oahu (type locality: Mount Tantalus). Molokai, Maui, Hawaii.

Hostplants: *Astelia menziesiana*, *Broussaisia*, *Metrosideros collina polymorpha* (sometimes found in abundance in the blossoms), *Vaccinium*.

Thrips (*Isoneurothrips*) *australis* Bagnall.*Thrips (Isoneurothrips) australis* Bagnall, 1915:592.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii.

Immigrant. Described from Australia and known from Tasmania. First found in the Hawaiian Islands by F. A. Bianchi in 1938 in the Honouliuli Forest Reserve, Oahu.

Hostplants: *Buddleia japonica*, *Eucalyptus robusta*, guava, *Leucaena glauca*, *Metrosideros*, *Pittosporum undulatum*. A flower species which evidently feeds on nectar.

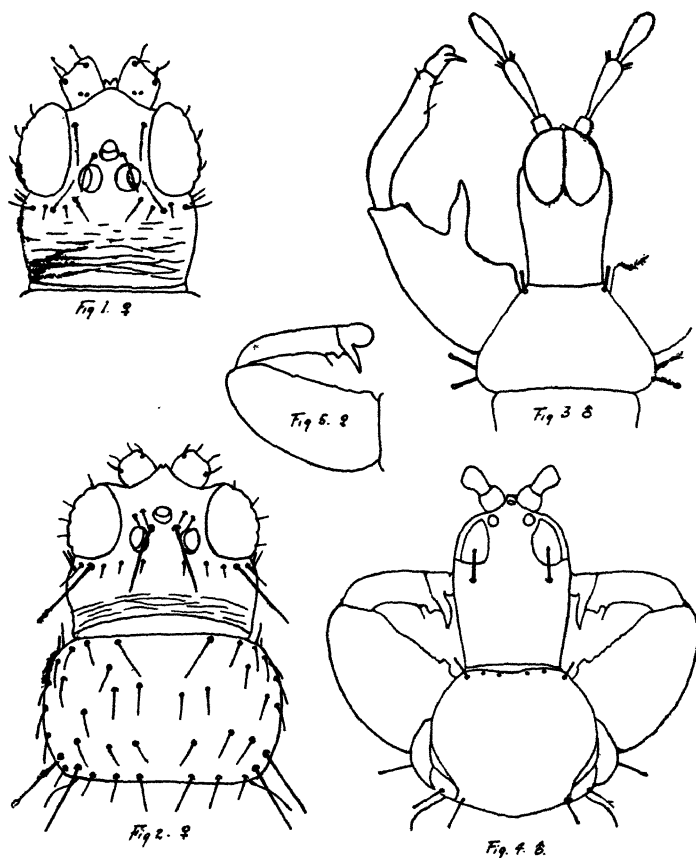


Figure 225—Details of some thrips: 1, *Thrips (Thrips) saccharoni* Moulton; 2, *Thrips (Isoneurothrips) fullawayi* (Moulton); 3, *Macrophthalmothrips hawaiiensis* Moulton; 4, *Podonthrips (Kentronothrips) lucaseni* (Krüger), with fore leg of female at 5. (After Moulton, 1928.)

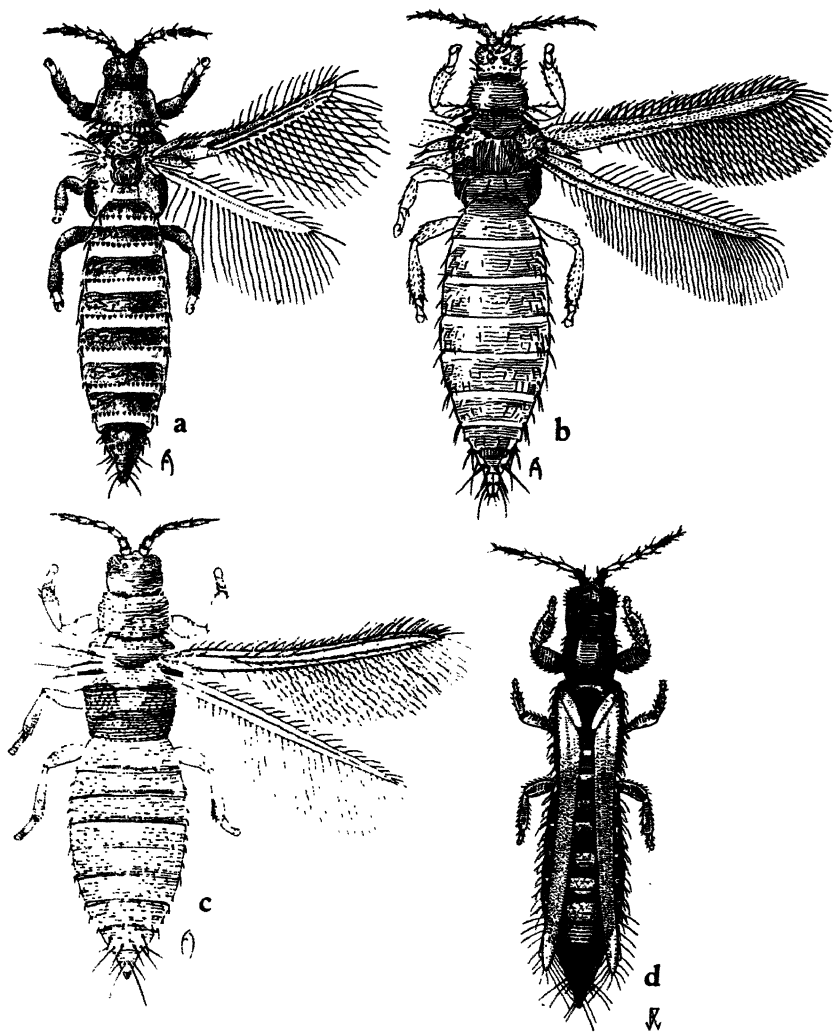


Figure 226—**a**, *Thrips* (*Microcephalothrips*) *abdominalis* (Crawford); **b**, *Thrips* (*Isoneurothrips*) *fullawayi* (Moulton); **c**, *Thrips* (*Thrips*) *tabaci* Lindeman; **d**, *Thrips* (*Thrips*) *saccharoni* Moulton. (Figure **d** by Williams, others by Abernathy; not to same scale.)

***Thrips* (*Isoneurothrips*) *carteri* (Moulton).**

Isoneurothrips carteri Moulton, 1937:411.

Endemic (?). Oahu (type locality: Kipapa), Hawaii.

Described from a unique specimen taken in a wind trap in a pineapple field. F. A. Bianchi found it associated with rust fungus on *Acacia koa* at Kilauea, Hawaii.

Thrips (Isoneurothrips) dubautiae (Moulton).

Isoneurothrips dubautiae Moulton, 1928:113.

Endemic (?). Oahu (type locality: Mount Tantalus).

Hostplants: *Dubautia*, *Delonix regia*.

Thrips (Isoneurothrips) fasciatus (Moulton).

Isoneurothrips fasciatus Moulton, 1937:410.

Endemic (?). Oahu (type locality: Kipapa).

Described from a unique specimen collected in a wind trap in a pineapple field.

Thrips (Isoneurothrips) fullawayi (Moulton) (figs. 225; 226, b).

Isoneurothrips fullawayi Moulton, 1928:114, pl. 1, fig. 2.

Endemic (?). Kauai, Oahu (type locality: Pauoa Valley).

Hostplants: *Broussonetia papyrifera*, *Broussaisia arguta* (in flower), *Ipomoea congesta*, *Pipturus* and other unrecorded hostplants. F. A. Bianchi found young and adults feeding on leaves of *Pipturus*.

Thrips (Isoneurothrips) multispinus (Bagnall).

Thrips multispinus Bagnall, 1910:699, pl. 17, figs. 15-20.

Endemic (?). Kauai, Oahu(?), Molokai, Maui(?), Hawaii (type locality not designated by Bagnall).

The male and female types and two cotype females are mounted on slides, and two cotype females are mounted on a card in the British Museum.

I have seen no authentic specimens of *Thrips multispinus* and have been unable to place it in the key. According to Moulton (1928:116), his *fullawayi* is close to *multispinus*. If his conclusions, based upon Bagnall's description only, are correct, then *multispinus* would evidently run to couplet six in the key. In a comparative table given by Moulton (1928:116), he notes that the female of *multispinus* is supposed to have the prothorax distinctly longer than the head, whereas the two are subequal in length in *fullawayi*, that the antennal style is one-fourth the length of segment six in *multispinus* and one-half the length of that segment in *fullawayi* and that *fullawayi* is 0.92 mm. long, whereas *multispinus* is only 0.65 mm. in length. Hood, in a letter to Bianchi, stated that he had examined one of Bagnall's original specimens, and that the example was closely similar to *fullawayi* but the antennae were stouter as in Bagnall's figure. I cannot help but believe that some synonymy is involved here and that one of the species names currently used in Hawaii really applies to Bagnall's *multispinus*.

Thrips (*Isoneurothrips*) *williamsi* (Moulton).

Isoneurothrips williamsi Moulton, 1928:115.

Endemic (?). Kauai, Oahu (type locality: Mount Tantalus), Hawaii.

Described from a unique specimen.

Hostplants: *Acacia koa*, *Metrosideros*, *Myoporum sandwicense*, *Sophora chrysophylla*; a flower species found on various plants in both lowlands and highlands.

Suborder TUBULIFERA Haliday, 1836

This suborder contains the largest of the Thysanoptera. In general, the species are of more cryptic habit than those of the Terrebrantia, and many live beneath dead bark, in dead wood, or in trash. Many are known to be predaceous or fungivorous. They usually are more sluggish than the members of the Terrebrantia, and many are restricted in their host preferences. This is the dominant group of thrips in our native forests.

The ovipositor is wanting in the members of this suborder and the females lay their eggs loosely about in cracks or on the surface of their place of abode; they are not inserted in plant tissues as are those of the Terrebrantia. The females may be distinguished by the fact that the ventral basal margin of the tube is entire, and there is a short, heavily sclerotized, longitudinal bar-like structure visible near the posterior edge of the ninth sternite. The males lack this structure, and the basal, ventral margin of the tube is emarginate.

KEY TO THE SUPERFAMILIES OF TUBULIFERA

1. Maxillary palpi two-segmented; antennae seven-, or usually eight-segmented; mid coxae more widely separated than other pairs; abdominal segment nine not or rarely longer than eight; caudal abdominal bristles rarely longer than tube..... **Phlaeothripoidea.**
2. Maxillary palpi one-segmented; antennae four- to seven-segmented; metacoxae more widely separated than fore or middle pairs; abdominal segment nine longer than eight; caudal abdominal bristles conspicuously longer than tube..... **Urothripoidea.**

Superfamily PHLAEOTHRIPOIDEA Hood, 1915:58

Haliday's original spelling of the type genus is *Phlaeothrips*, not *Phloeothrips* as was used by Burmeister in his *Handbuch* in 1838 and by many subsequent authors.

Family PHLAEOTHRIPIDAE Uzel, 1895

The arrangement of this family is in chaos. I have been unable to use the characters given by any author to separate the various Hawaiian representatives into the described subfamilies and tribes. The classifications followed by Hinds,

Karny (adapted by Watson) and Priesner differ in almost every way. It has been impossible to fit many genera into Watson's translations (1923) of Karny's keys (1921). It is, I believe, the task of a skilled, broadly trained specialist in the Thysanoptera to present an adequate classification and arrangement of the Hawaiian Phlaeothripidae, for such a revision is beyond the scope of this volume and beyond my present ability and experience. I have, therefore, drawn up a tentative key to the genera from Hawaiian material and have not attempted to follow the key characters used by other workers. If this text will enable local workers to place their species, its purpose will be satisfied.

According to Priesner's work (1928), the genera of Tubulifera found in Hawaii would be arranged as follows:

Phlaeothripoidea

Phlaeothripidae

Phlaeothripinae

Phlaeothripini

Phlaeothrips Haliday.

Hoplothripini

Agnostochthona Kirkaldy.

Dermothrips Bagnall.

Hoplothrips Amyot and Serville.

Liothrips Uzel.

Macrophthalmothrips Karny.

Nesothrips Kirkaldy.

Polyporothrips Watson.

Haplothripini

Aleurodothrips Franklin.

Haplothrips Amyot and Serville.

Karnyothrips Watson.

Podothrips Hood.

Megathripinae

Compsothripini

Rhaebothrips Karny.

Dichaetothrips Hood.

Diceratothrips Bagnall

Urothripoidea

Urothripidae

Stephanothrips Trybom.

Conocephalothrips Bianchi.

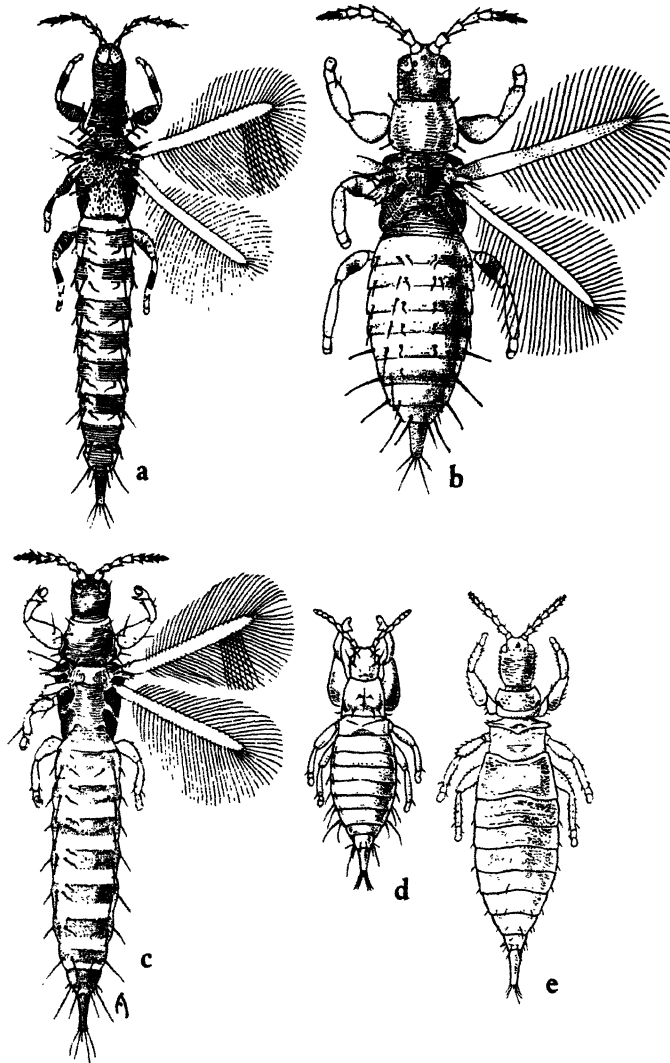


Figure 227—*a*, *Macrophthalthothrips hawaiiensis* Moulton; *b*, *Aleurodothrips fasciapennis* (Franklin); *c*, *Hoplothrips flavitibia* Moulton; *d*, *Nesothisrips oahuensis* Kirkaldy (redrawn from Bagnall, 1910); *e*, *Dermothrips hawaiiensis* Bagnall (redrawn from Bagnall, 1910). (Abernathy drawings.)

KEY TO THE GENERA OF PHLAEOTHRIPIIDAE FOUND IN HAWAII

1. Anterior part of head peculiarly formed (see fig. 227, a), eyes large, subcontiguous behind, first antennal segments concealed from above. **Macrophthalmothrips** Karny.
Without such a combination of characters. 2
- 2(1). The long setae at hind prothoracic angles simple at apices. 3
The long setae at hind prothoracic angles capitate. 9
- 3(2). Sides of head (cheeks) coarsely granular or papillate, some granules or warts bearing spines; three distal antennal segments closely united, sometimes appearing to be a single segment. **Dermothrips** Bagnall.
Sides of head at most finely granular and without setiferous papules; antennal segment seven always distinctly separated from six. 4
- 4(3). Head not much longer than prothorax (fore femora of male greatly enlarged). **Nesothrips** Kirkaldy.
Head conspicuously longer than prothorax. 5
- 5(4). Sides of head, femora and tibiae with several or many long, stout spines or comparatively long, stout spines. 6
Sides of head, femora and tibiae with few or no stout spines, those present fine. 7
- 6(5). Antecellar bristles more prominent than postocellars.
. **Diceratothrips** Bagnall.
Postocellar bristles more prominent than antecellars.
. **Dichaetothrips** Hood.
- 7(5). Fore tarsi armed with a strongly developed thumb-like tooth (except in *Hoplothrips paumalui*, but that species has most antennal segments dark instead of pale as in our *Liothrips*, and the head is not much longer than broad; the shorter head and pointed mouth cone will separate it from *Rhaebothrips*).
. **Hoplothrips** Amyot and Serville.
Fore tarsi unarmed. 8
- 8(7). Mouth cone sharply pointed. **Liothrips** Uzel.
Mouth cone bluntly rounded. **Rhaebothrips** Karny.
- 9(2). Sides of head (cheeks) with bristle-bearing tubercles or papules. **Phlaeothrips** Haliday.
Sides of head without bristles-bearing tubercles. 10
- 10(9). Eighth antennal segment distinctly pedicellate at base (segments three to seven also pedicellate).
. **Polyporotheis** Watson.
Eighth antennal segment broadly joined at the base to seven and not pedicellate. 11
- 11(10). Head with length of dorsal exposed part to apex of inter-antennal process not as great or only slightly greater than extreme breadth. 12
Exposed part of head distinctly longer than broad, as much as one-third longer than broad. 13

- 12(11). Third antennal segment cone-shaped or subglobular and but little longer than broad; wings not banded in our species **Haplothrips** Amyot and Serville.
Third antennal segment obviously elongate, about twice as long as broad; wings banded in our species.....
..... **Aleurodothrips** Franklin.
- 13(11). Entirely dark species; fore legs armed with a long, strong, projecting tooth on basal tarsal segment and one or two small denticles near apex of each tibia; fore femora normally with a blunt, subbasal tooth on inner margin....
..... **Podothrips** Hood.
Species at least partly pale; fore femora and tibiae unarmed; fore tarsus with a comparatively small subapical tooth **Karnyothrips** Watson.

Genus **PHLAEOTHRIPS** Haliday, 1836:441

Phlocothrips Burmeister, 1838.

KEY TO THE SPECIES FOUND IN HAWAII

1. Mouth cone not unusually elongate, not extending beyond prosternum **claratibia** Moulton.
2. Mouth cone unusually elongate, reaching about to middle of mesosternum **mauiensis** Moulton.

Phlaeothrips claratibia Moulton (fig. 216, a).

Phlocothrips claratibia Moulton, 1937:414.

Oahu (type locality: Kipapa).

Immigrant, but not yet recorded elsewhere.

Hostplants: on the leaves of pineapple, *Pritchardia* and *Pandanus*.

Phlaeothrips mauiensis Moulton (fig. 219).

Phlocothrips mauiensis Moulton, 1928:130.

Oahu, Maui (type locality: Olinda), Hawaii.

Immigrant, but not yet known elsewhere.

Hostplants: *Acacia koa* (under dead bark), *Ipomoea*, *Pittosporum confertiflorum*, *Sophora chrysophylla*.

Genus **LIOTHRIPS** Uzel, 1895

Liothrips floridensis (Watson).

Cryptothrips floridensis Watson, 1913:145, pl. 6, figs. 1-4.

Liothrips floridensis (Watson) Hood, 1918:132.

The camphor thrips.

Oahu.

Immigrant. Described from camphor from Florida. First recorded from the Hawaiian Islands by Swezey in 1939 from specimens collected in Honolulu in 1938.

Hostplant: camphor; infests the buds, killing some and deforming the leaves.

Genus **POLYPOROTHRIPS** Watson, 1927

Polyporothrips biformis (Moulton).

Poecilothrips biformis Moulton, 1934:501.

Polyporothrips biformis (Moulton) Moulton, 1936:187.

Oahu (type locality: Honolulu).

Immigrant (?).

Only females of this species are known, and they may or may not have wings. The type series was taken from a decaying stump.

Genus **MACROPHTHALMOTHRIPS** Karny, 1922

Ophthalmothrips Karny, 1920, not Hood, 1919.

Macrophthalthrips hawaiiensis Moulton (figs. 225; 227, a).

Macrophthalthrips hawaiiensis Moulton, 1928:122, pl. 1, fig. 3.

Kauai, Oahu, Maui (type locality: Olinda), Hawaii.

Immigrant, but not yet recorded elsewhere.

Hostplants: *Acacia koa* (under dead bark), *Perottetia sandwicensis*, *Sophora chrysophylla*, *Sapindus saponaria*, *Xylosma hawaiiensis* var. *hillebrandii*.

Genus **NESOTHRIPS** Kirkaldy, 1907:103

Oedemothrips Bagnall, 1910:680. Synonymy and redescription by Bianchi, 1944:31.

This genus is known elsewhere from New Zealand, Australia, Japan and Ceylon.

Nesothrips oahuensis Kirkaldy (fig. 227, d).

Nesothrips oahuensis Kirkaldy, 1907:103. Genotype.

Oedemothrips laticeps Bagnall, 1910:680, pl. 17, figs. 6, 10. Genotype of *Oedemothrips*. Synonymy and redescription by Bianchi, 1944:32, pl. 1. The dry, card-mounted type and a slide-mounted cotype female are in the British Museum.

Nesothrips hawaiiensis, name cited in error by Bianchi, 1944:31. Bianchi, 1945:279, emended description.

Endemic (?). Oahu (type locality: Mount Tantalus), Molokai, Lanai.
Hostplant: *Carex wahuensis*.

Genus **DERMOTHRIPS** Bagnall, 1910:677

This genus has not yet been reported from outside the Hawaiian Islands.

Dermothrips hawaiiensis Bagnall (fig. 227, e).

Dermothrips hawaiiensis Bagnall, 1910:678, pl. 17, figs. 1, 5. Genotype.

Endemic (?). Kauai, Oahu, Maui, Hawaii.

Hostplant: *Myrsine* (*Suttonia*) (under dead bark).

Both macropterous and brachypterous forms of this species have been found.

The card-mounted holotype male is in the British Museum, as are three slides of cotype females (apterous) and one slide-mounted macropterous female.

Genus **HOPLOTHRIPS** Amyot and Serville, 1843

Dolerothrips Bagnall, 1910:682. Synonymy by Hood, 1915:105.

The situation existing as to the status of the species of this genus is too involved to be clarified in this work. It is next to impossible, if not completely impossible, to straighten out the group without gathering together all of the types and a series of fresh material and making a detailed study of each species.

Bagnall, in *Fauna Hawaïensis*, originally assigned nine species to *Dolerothrips* and two to *Trichothrips*. These 11 species are now included in *Hoplothrips*, which is a taxonomically difficult assemblage of species. Most or all of Bagnall's material consisted of card-mounted, dried specimens, and six of his 11 species were founded upon unique specimens, some of which were imperfect. In recent years Moulton has added six species to bring the list of Hawaiian *Hoplothrips* to 17. Moulton evidently could not identify Bagnall's species from the literature, and apparently described most of the various species coming to him for identification as new species in an attempt to make a fresh start on the Hawaiian *Hoplothrips*. In doing so, however, it appears that he has redescribed some of Bagnall's species. This, in brief, is an outline of the difficult situation confronting us in our study of local *Hoplothrips*.

Bagnall (1910:683) gave a key to include all but one of his new species of *Dolerothrips* and *Trichothrips* (p. 692). I have recast his key to include all of his 11 species. The new key may aid in separating a collection of *Hoplothrips* into species which, through more detailed study and comparison, might be specifically identified or placed with a group of species or shown *not* to be certain species. The reader should understand that this key has not been tested, and it may prove to be not workable when adequate material is assembled.

KEY TO THE SPECIES OF HOPLOTHIRIPS DESCRIBED BY BAGNALL

1. Head as broad as long or very nearly as broad as long..... 2
Head longer than broad..... 3
- 2(1). Chestnut brown; posterior ocelli remote from inner margins of eyes; tube four-fifths as long as head and three times as long as breadth at base..... **laticornis** (Bagnall).
Black; posterior ocelli touching inner margins of eyes; tube less than two-thirds as long as head and only twice as long as breadth of base..... **nigricans** (Bagnall).
- 3(1). All femora yellow..... **flavipes** (Bagnall).
All femora concolorous with body..... 4
- 4(3). Abdominal bristles abbreviated or obsolete..... 5
Abdominal bristles well developed..... 6
- 5(4). Abdominal bristles abbreviated (tube short and broad)...
..... **intermedius** (Bagnall).
Abdominal bristles obsolete..... **lanaiensis** (Bagnall).
- 6(4). Length 3.5 mm.; cheeks slightly swollen and spinose near posterior third..... **barbatus** (Bagnall).
Length 1.6-2.5 mm.; cheeks more or less evenly spinose.... 7
- 7(6). Abdomen dark-brown, tube pale reddish-brown, almost as long as head..... **bicolor** (Bagnall).
Abdomen and tube concolorous; tube distinctly shorter than head..... 8
- 8(7). Tube about twice as long as its basal breadth..... 9
Tube about three times as long as its basal breadth..... 10
- 9(8). Antennae with basal part of segment three yellowish, remainder dark in color..... **perkinsi** (Bagnall).
Antennae with parts of segments three to five yellowish...
..... **dubius** (Bagnall).
- 10(8). Head long and narrow, one and one-half times as long as broad..... **angusticeps** (Bagnall).
Head only a little longer than broad..... **ovatus** (Bagnall).

The species described by Moulton might be separated by the following key which I have drawn up partly from his descriptions.

KEY TO THE HAWAIIAN HOPLOTHIRIPS DESCRIBED BY MOULTON

1. "A pair of very weak wing retaining spines on abdominal segments three to seven and a single long prominent spine near posterior margin on each side, the regular spines vestigial"..... **hawaiiensis** Moulton.
Not so, the spines developed and/or with two prominent spines near posterior margin..... 2
- 2(1). Wings clear; fore tarsi unarmed..... **paumalui** Moulton.
Wings grayish-brown; fore tarsi armed with a tooth..... 3
- 3(2). Outer outline of eyes flattened..... **coprosmae** Moulton.
Outer outline of eyes obviously convex..... 4
- 4(3). Antennae somewhat more than twice as long as head, segment eight spindle-shaped; tibiae yellow.....
..... **flavitibia** Moulton.

- Antennae about twice as long as head or less than twice as long as head, segment eight spindle-shaped or not; tibiae brown or brownish 5
- 5(4). Eighth antennal segment spindle-shaped and obviously narrower than seven *mauiensis* Moulton.
Eighth antennal segment stout, not spindle-shaped, but slightly narrower than seven *swezeyi* Moulton.

***Hoplothrips angusticeps* (Bagnall).**

Dolerothrips angusticeps Bagnall, 1910:688, pl. 18, figs. 20-22.

Hoplothrips angusticeps (Bagnall) Hood, 1915:105.

Endemic. Molokai (type locality: Kalae?).

The card-mounted type is in the British Museum.

***Hoplothrips barbatus* (Bagnall).**

Dolerothrips barbatus Bagnall, 1910:683, pl. 18, figs. 11-14.

Hoplothrips barbatus (Bagnall) Hood, 1915:105.

Endemic. Hawaii (type locality: Kona, 4,000 feet).

Known only from the unique male type which was found beneath a decaying log. This specimen is mounted on a slide in the British Museum.

***Hoplothrips bicolor* (Bagnall).**

Dolerothrips bicolor Bagnall, 1910:688, pl. 19, figs. 21-22.

Hoplothrips bicolor (Bagnall) Hood, 1915:105.

Endemic. Oahu (type locality: "Kaala Mts., over 2000 ft.").

The dry holotype is mounted on the same card as *Hoplothrips nigricans* ("Trichothrips") in the British Museum.

***Hoplothrips coprosmae* Moulton.**

Hoplothrips coprosmae Moulton, 1936:186.

Endemic. Kauai, Oahu, Maui, Hawaii (type locality: Nauhi).

Hostplants: *Coprosma* (type series from cracks in stem), *Dodonaea*.

Moulton, in his original description, stated that the head of this species was 1.4 times as long as broad. However, measurements of two of the paratypes reveal that the head is only 1.1 times as long as broad.

***Hoplothrips dubius* (Bagnall).**

Dolerothrips dubius Bagnall, 1910:691, pl. 19, figs. 23-27.

Hoplothrips dubius (Bagnall) Hood, 1915:105.

Endemic. Molokai, Lanai, Hawaii (type locality not designated by Bagnall).
The card-mounted type is in the British Museum.

Hoplothrips flavipes (Bagnall) (figs. 216, b; 219).

Dolerothrips flavipes Bagnall, 1910:685, pl. 18, figs. 15–19. Genotype of *Dolerothrips*.

Hoplothrips flavipes (Bagnall) Hood, 1915:105.

Dolerothrips japonicus Karny, Arkiv für Naturgeschichte, 79A:126, 1913. Synonymy by Hood, 1939:587.

Trichothrips karnyi major Hood, 1914:153. Synonymy by Hood, 1939:587.

Maui (type locality: Haleakala).

Immigrant. Known also from Japan and introduced into the United States. See Hood, 1939:587, footnote 5.

Part of the type series was found under dead bark at 5,000 feet, but apparently the type locality is 3,000 feet. A slide marked "Cotype, Haleakala, Maui, 3000 ft., IV, 1894," is in the British Museum as are four other slides.

I am not sure that Hood's synonymy is correct, and this may be an endemic species.

Hoplothrips flavitibia Moulton (fig. 227, c).

Hoplothrips flavitibia Moulton, 1928:117.

Kauai, Oahu (type locality not designated in the original description), Maui, Hawaii.

Immigrant. Moulton (1939:144) identified material I collected at Tahiti and in the Austral Islands as this species, but the specimens should be checked carefully.

Hostplants: *Acacia koa*, *Aleurites moluccana*, *Auricularia* (an edible fungus), *Eucalyptus*, *Eugenia cumini* (Java plum), *Prosopis*, *Myrsine* (*Suttonia*) (under dead bark and in insect burrows).

Hoplothrips hawaiiensis Moulton.

Hoplothrips hawaiiensis Moulton, 1936:185.

Endemic. Oahu (type locality: Mount Tantalus), Maui.

Hostplants: *Cibotium menziesii* (in dead fronds), "tree ferns," *Metrosideros*.

Hoplothrips intermedius (Bagnall).

Dolerothrips intermedius Bagnall, 1910:689, pl. 19, figs. 7–9.

Hoplothrips intermedius (Bagnall) Hood, 1915:105.

Endemic. Maui (type locality: Haleakala, 3,000 feet).

The dried type is in the British Museum.

Hoplothrips lanaiensis (Bagnall).

Dolerothrips lanaiensis Bagnall, 1910:690, pl. 19, figs. 10-16.

Hoplothrips lanaiensis (Bagnall) Hood, 1915:105.

Endemic. Molokai, Lanai, Hawaii (type locality not designated in original description).

The card-mounted type is in the British Museum.

Hoplothrips laticornis (Bagnall).

Trichothrips laticornis Bagnall, 1910:692, pl. 18, figs. 6-10.

Hoplothrips laticornis (Bagnall) Moulton, 1928:133.

Endemic. Hawaii (type locality: Kona, 3,000 feet).

Dr. Laing reports that the type has never been traced and that "This was a single female in spirit; it is also a figured species and I suspect that it was never returned to Bagnall by the artist."

Hoplothrips mauiensis Moulton (fig. 216, c).

Hoplothrips mauiensis Moulton, 1928:119.

Endemic. Oahu, Maui (type locality: Olinda).

Hostplant: *Acacia koa* (under bark).

Hoplothrips nigricans (Bagnall).

Trichothrips nigricans Bagnall, 1910:693, pl. 18, fig. 23.

Hoplothrips nigricans (Bagnall) Moulton, 1928:134.

Endemic. Oahu (type locality: "Kaala Mts., over 2000 ft.").

The type is mounted dry on a card in the British Museum.

Hoplothrips ovatus (Bagnall).

Dolerothrips ovatus Bagnall, 1910:686, pl. 18, figs. 1-6.

Hoplothrips ovatus (Bagnall) Hood, 1915:105.

Endemic. Maui (type locality: Haleakala, 5,000 feet).

The card-mounted type is in the British Museum together with one other slide.

Hoplothrips paumalui Moulton.

Hoplothrips paumalui Moulton, 1937:412.

Oahu (type locality: Paumalu).

Immigrant (?).

Hostplants: *Emilia sonchifolia*, *Lantana camara*, *Paspalum conjugatum*.

This is the only one of our *Hoplothrips* which has the fore tarsi unarmed and the wings clear.

***Hoplothrips perkinsi* (Bagnall).**

Dolerothrips perkinsi Bagnall, 1910:687, pl. 19, figs. 17-20.

Hoplothrips perkinsi (Bagnall) Hood, 1915:105.

Endemic. Lanai (type locality: 2,000 feet).

The card-mounted type is in the British Museum.

***Hoplothrips swezeyi* Moulton.**

Hoplothrips swezeyi Moulton, 1928:120.

Endemic. Maui (type locality: Olinda).

Hostplants: under dead bark and in dead wood of *Metrosideros*, *Myrsine*, *Pipturus*, *Rubus hawaiiensis*.

GENUS INCERTAE SEDIS

Genus **AGNOSTOCHTHONA** Kirkaldy, 1907:102

This genus has not been recognized in any Hawaiian material collected since its description appeared. The type was probably point-mounted, as was Kirkaldy's type of *Nesothrips*, and it may have been lost or destroyed. Bagnall (1910:694) could not recognize it, and he said that the characters given by Kirkaldy in his description "are much too meagre upon which to erect a genus: in fact as the description now stands the type species may be relegated to any one of several genera, not a single character of generic value is emphasized in the diagnosis. From the short specific description it is clear that the species is not represented in the collection made by Dr. Perkins. As yet we have not had the opportunity of examining Kirkaldy's types; this will be necessary before its true position can be made clear."

In my opinion, *Agnostochthona* may be a synonym of *Hoplothrips*, and its genotype may be a synonym of one of the common species found at the type locality. However, Karny (1921:38) assigned a new species from Java (on *Hevea* rubber) to this genus. It is possible that Karny's species is not congeneric with that of Kirkaldy.

***Agnostochthona alienigera* Kirkaldy.**

Agnostochthona alienigera Kirkaldy, 1907:102. Genotype.

Endemic (?). Oahu (type locality: Mount Tantalus).

Habit: found under the bark of a dead tree.

Genus **ALEURODOTHrips** Franklin, 1909**Aleurodothrips fasciapennis** (Franklin) (fig. 227, b).*Cryptothrips fasciapennis* Franklin, 1908:727, pl. 64, figs. 12, 13.

Oahu.

Immigrant. Widespread; described from the West Indies. First recorded from Hawaii by Moulton (1936:187) from specimens taken from a coconut from Honolulu intercepted in quarantine at San Francisco.

Hosts: predaceous on aleurodids, crawlers of coccids, including *Diaspis echinocacti* on *Epiphyllum*, and probably on aphids; also found on coconut, *Ficus bengalensis*.

Genus **KARNYOTHRIPS** Watson, 1923:70*Karnyia* Watson, 1922, preoccupied.

Some workers refer this group to *Haplothrips*, as a subgenus.

KEY TO THE SPECIES FOUND IN HAWAII

1. Conspicuously bicolored, most of abdomen obviously paler than apex or head and thorax.....**melaleuca** (Bagnall).
Dark brown, not distinctly bicolored..... 2
2. Antennal segments three and four rather similar in shape, three narrowed from near apex to base and subtriangular in outline**flavipes** (Jones).
Third and fourth antennal segments conspicuously different in shape, three very broad and subtruncate at base, more subparallel-sided than subtriangular in shape.....
.....**dolicornis** Bianchi.

Karnyothrips dolicornis Bianchi.*Karnyothrips dolicornis* Bianchi, 1946:510, pl. 30, figs. A, B, C.

Hawaii (type locality: Makaopuhi, 2,870 feet).

Immigrant (?).

Hostplants: *Metrosideros*, *Myoporum sandwicense*, *Myrsine lessertiana*, *Sadleria*, *Sophora chrysophylla*.

Karnyothrips flavipes (Jones).*Anthothrips flavipes* Jones, 1912:18, pl. 5, figs. 5-7.*Haplothrips* (*Karnyothrips*) *flavipes* (Jones), of authors.

Oahu, Hawaii.

Immigrant. Widespread. First recorded from the Hawaiian Islands by Moulton (1936:187) from specimens collected on Oahu by Swezey in 1933 and 1934.

Hostplants: *Acacia koa*, *Coprosma*, *Euphorbia*, *Lantana* (blossoms), *Macaranga*, *Metrosideros*, *Mezouneuron kauaiense*, *Myoporum sandwicense*, *Myrsine lessertiana*. It is a predator. Bianchi (1945:279) found them in old oothecae of the mantid *Tenodera angustipennis*.

Karnyothrips melaleuca (Bagnall).

Hindsiana melaleuca Bagnall, 1911:61.

Dolerothrips carteri Watson, a manuscript name and misidentification in Ito and Carter, 1932:44.

Kauai, Oahu, Hawaii.

Immigrant. Widespread; described from a unique specimen taken from a hot-house crucifer at Copenhagen. First recorded from Hawaii by Moulton (1934:502) from specimens collected on Oahu by Carter and Illingworth.

Hostplants: *Bothriospermum tenellum*, *Cibotium chamissoi*, *Coronopus didymus* (*Senebiera didyma*), *Digitaria sanguinalis*, *Emilia* species, *Heimerliodendron brunonianum*, Job's tears, pineapple, *Pittosporum confertiflorum*, sugarcane, *Tricholaena repens* (*roscia*). Evidently a predaceous species which feeds upon "red spiders."

Genus **PODOTHRIPS** Hood, 1913

Subgenus **Kentronothrips** (Moulton, 1928:126) Priesner, 1938:68

Podothrips (Kentronothrips) lucasseni (Krüger) (figs. 225, 228).

Phloeothrips Lucasseni Krüger, 1890:105, pl. 3B, figs. 8-9.

Kentronothrips hawaiiensis Moulton, 1928:126, pl. 1, figs. 4, 5. 1940:268. Genotype of *Kentronothrips*. For detailed redescription and synonymy, see Priesner, 1938:68, figs. 1-2.

Kauai, Oahu, Hawaii.

Immigrant. Widespread in the Indo-Pacific regions. First recorded from the Territory by Moulton (1928:126, as *Kentronothrips hawaiiensis*) from specimens intercepted in quarantine in San Francisco in 1909 on sugarcane from Honolulu and from material collected by Swezey in 1927.

Hostplants: sugarcane (common behind leaf sheaths), sour grass (*Trichachne insularis* [*Valota insularis*]).

A predator on the stalk mite, *Tarsonemus spinipes* Hirst.

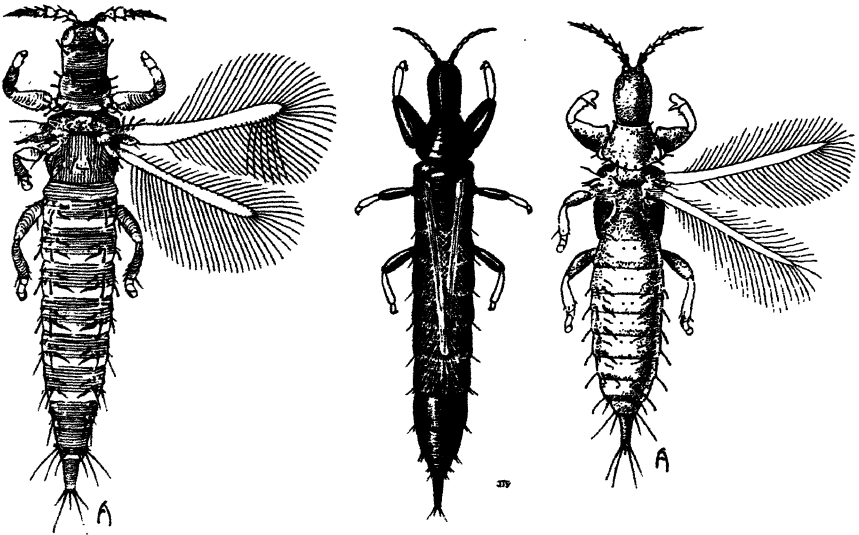


Figure 228—*Haplothrips* (*Haplothrips*) *gowdeyi* (Franklin), left (wings reconstructed); *Podothrips* (*Kentranothrips*) *lucasseni* (Krüger), middle and right (the middle figure is of a fresh example, the one on the right is from a slide mount). (Middle figure after Williams, 1931; others by Abernathy; not to same scale.)

Genus **HAPLOTHRIPS** Amyot and Serville, 1843

It is unfortunate that the authors of this genus should have also chosen to erect so similar a name as *Hoplothrips*, because considerable confusion occurs in the use of the names.

KEY TO THE SPECIES OF HAPLOTHRIPS FOUND IN HAWAII

1. Fore tarsi armed with one or two small claws; dark-colored species 2
- Fore tarsi evidently unarmed; body at least partly pale..... 5
- 2(1). Large setae behind middle of prothorax with blunt or expanded tips 3
- These setae fine and with slender sharp tips..... 4
- 3(2). Third antennal segment with three sense cones, one of which is on the inner (anterior) face of the segment (thus a sense cone is visible on both the inner and outer sides of the segment); large postero-lateral dorsal abdominal spines dark **gowdeyi** (Franklin).
- Third antennal segment with only one sense cone, and that on the outer (posterior) face (thus only one sense cone is visible in the same plane of focus); large postero-lateral dorsal abdominal spines pale..... **fusca** Moulton.

- 4(2). Antero-marginal setae of pronotum all minute. . . . **rosai** Bianchi.
 Outer antero-marginal setae of pronotum as long as antero-
 angulars **davisi** Bianchi.
- 5(1). Body conspicuously bicolored; head, thorax and abdominal
 segments eight to ten dark, remainder of abdomen pale;
 antennae with segments three to six paler than others . . .
 **sakimurai** Moulton.
 Body not strikingly bicolored; antennal segments two and
 three only pale **williamsi** Moulton.

Subgenus **Haplothrips** Amyot and Serville

Haplothrips (Haplothrips) davisi Bianchi.

Haplothrips davisi Bianchi, 1946:503, pl. 29, fig. D; pl. 30, fig. D.

Endemic (?). Hawaii (type locality: Mauna Loa truck trail, 6,500 feet).

Hostplants: *Acacia koa*, *Metrosideros*, *Pipturus*, *Sophora chrysophylla*. Found on leaves and dead branches.

Bianchi (1946:506) says, "from other species found in Hawaii it can be separated easily by its long pointed setae, of which only the anteroangulars and anteromarginals on the pronotum are likely to be, but are not always, slightly expanded at the end."

Haplothrips (Haplothrips) fusca Moulton.

Haplothrips (Haplothrips) fusca Moulton, 1928:124.

Oahu (type locality: Fort Kamehameha), Molokai.

Immigrant, but not yet known elsewhere.

Hostplants: *Batis maritima*, *Cladium angustifolium* (sedge).

Haplothrips (Haplothrips) gowdeyi (Franklin) (fig. 228).

Anthothrips gowdeyi Franklin, 1908:724, pl. 63, fig. 8; pl. 64, figs. 15, 16; pl. 65, fig. 23.

Anthothrips usitatus Bagnall, 1910:695, pl. 17, figs. 16-17 (type series from Hilo grass at Kona, Hawaii, 2,000 feet, collected by Perkins in 1892). Synonymy by Moulton, 1934:502. Bagnall's type series, a slide containing the male and female types, a slide containing a male and female cotype and a slide containing two cotype females are in the British Museum.

The black flower thrips.

Kauai, Oahu, Molokai, Lanai, Maui, Hawaii, Midway.

Immigrant. Cosmopolitan. First recorded from the Hawaiian Islands by Bagnall (1910:695, as *Anthothrips usitatus*) from specimens taken by Perkins on Hawaii in 1892.

Hostplants: This species is commonly found in clusters of flowers. *Acacia farnesiana*, *Ageratum conyzoides*, alfalfa, *Amaranthus hybridus*, *Amaranthus viridis* (*gracilis*) (misidentified as *A. retroflexus*), *Argemone alba* var. *glauca* (prickly poppy), *Aster*, *Bidens pilosa*, *Bothriospermum tenellum*, *Brassica* ("shirona"), *Buddleia japonica*, *Cajanus cajan*, canna, carrot, *Cassia leschenaultiana* (misidentified as *mimosoides*), *Cassia occidentalis*, *Cenchrus echinatus*, *Chenopodium album* var. *candicans*, *Chloris inflata* (*paraguayensis*), *Chloris radiata*, cockscomb, *Comelina diffusa* (*nudiflora*), *Coronopus didymus* (*Senebiera didyma*), cotton, *Crotalaria juncea*, *Crotalaria mucronata* (*saltiana*), *Cucumis dipsaceus*, *Cyperus rotundus*, dandelion (*Taraxacum officinale*), *Digitaria pruriens*, *Digitaria sanguinalis* (*Syntherisma sanguinalis*), *Dioclea violacea*, *Echinochloa crus-galli*, eggplant, *Emilia coccinea*, *Emilia sonchifolia*, *Eragrostis cilianensis*, *Eragrostis variabilis*, *Erigeron albidus*, *Erigeron canadensis*, *Euphorbia geniculata*, *Gaillardia pulchella*, *Hippobroma longiflora* (*Isotoma longiflora*), *Hymenocallis declinata*, *Hypochaeris radicata*, *Ipomoea cairica*, *Ipomoea pes-caprae*, *Lantana camara*, lettuce, *Leucaena glauca*, *Malva*, *Mimosa pudica*, *Mirabilis jalapa*, onion, *Operculina aegyptia* (*Ipomoea pentaphylla*), *Panicum purpurascens* (*bardinode*), *Panicum torridum*, *Paspalum conjugatum*, *Paspalum dilatatum*, *Paspalum orbiculare*, *Phaseolus lathyroides*, *Phytolacca octandra* (misidentified as *acinosa*), pineapple, *Plantago lanceolata*, *Plantago major*, *Pluchea indica*, *Portulaca oleracea*, *Prosopis chilensis*, *Raphanus sativus*, *Richardsia scabra* (*Richardsonia scabra*), *Salvia leucantha*, *Setaria geniculata*, *Setaria verticillata*, *Solanum nodiflorum*, *Stachys arvensis*, *Stachytarpheta cayennensis* (*dichotoma*), *Tephrosia purpurea* (*piscatoria*), *Tithonia rotundifolia*, tomato, *Tribulus cistoides* ("nohii"), *Trichachne insularis*, *Tricholaena repens* (*rosea*), *Trisetum glomeratum*, *Verbena litoralis* (misidentified as *bonariensis*), *Verbesina encelioides*, *Vernonia cinerea*, *Waltheria americana*, *Zinnia pauciflora*.

Haplothrips (Haplothrips) rosai Bianchi.

Haplothrips rosai Bianchi, 1946:506, pl. 29, figs. A, B, C; pl. 30, fig. E.

Endemic (?). Hawaii (type locality: Makaopuhi, 2,870 feet).

Hostplants: *Metrosideros*, *Myrsine*, *Sadleria*, *Vaccinium*. Found on leaves, dead branches and fern fronds.

Subgenus **Hindsiana** Karny, 1910

Haplothrips (Hindsiana) sakimurai Moulton.

Haplothrips (Hindsiana) sakimurai Moulton, 1937:412.

Endemic (?). Kauai, Oahu (type locality: Kipapa), Hawaii.

Hostplants: *Cyperus rotundus* (nutgrass), *Emilia sonchifolia*, *Myoporum sandwicense*.

Haplothrips (Hindsiana) williamsi Moulton.

Haplothrips (Hindsiana) williamsi Moulton, 1934:502.

Endemic (?). Hawaii (type locality: Mount Hualalai).

Hostplants: under dead bark of *Diospyros (Maba)*, *Rubus hawaiiensis*, *Myrsine lessertiana*.

Genus RHAEBOTHRIPS Karny, 1913**Rhaebothrips major** Bagnall (fig. 223, A-C).

Rhaebothrips major Bagnall, 1928:75. Bianchi, 1945:280, pl. 17, figs. A, B, C; redescription.

Oahu.

Immigrant. Described from Samoa and known from Fiji. First reported from the Hawaiian Islands by Bianchi in 1945 from specimens collected in Honolulu in 1944.

Hostplants: it has been found in colonies in the hollow stems of *Merremia (Ipomoea) tuberosa* (wood rose), papaya and pigeon pea.

Genus DICERATOTHRIPS Bagnall, 1908**Diceratothrips brevicornis** Bagnall.

Diceratothrips brevicornis Bagnall, 1910:697, pl. 18, figs. 1-3. Moulton, 1936:187.

Oahu (type locality: Kawaihoa Gulch mountains).

Immigrant (?).

Hostplant: *Osteomeles* (under bark).

This species was described from an unique female (which is mounted dry on a card in the British Museum). The only other record of the species is that of Moulton (1936:187), who recorded a specimen found under *Osteomeles* bark in Manoa Valley, Oahu, September, 1929, by Swezey. This species remains unknown to resident thysanopterists in Honolulu, and there seems to be some doubt that the species is distinct from *Dichaetothrips setidens* (Moulton). In answer to my query as to how the species differed, Moulton, in 1944, said that he felt that they were distinct forms. He also stated that "The principal character separating the two genera... is the development of the ante-ocellar and post-ocellar setae. In *Diceratothrips* the ante-ocellars are usually strongly developed while in *Dichaetothrips* the post-ocellars are the most prominent... In *Dichaetothrips* the post-ocellars are sometimes almost as long as the postoculars and quite prominent while the ante-ocellars are very small or wanting... but at best it is sometimes almost impossible to distinguish between the two genera."

Genus **DICHAETOTHRIPS** Hood, 1914

In addition to the following species, Bianchi has specimens of another species from Oahu which is as yet undetermined.

KEY TO THE SPECIES FOUND IN HAWAII

1. Wings comparatively clear, not clouded.....**claripennis** Moulton.
2. Wings infusate, with dark vittae.....**setidens** (Moulton).

Dichaetothrips claripennis Moulton.

Dichaetothrips claripennis Moulton, 1934:503.

Oahu (type locality: Honolulu).

Immigrant, but not yet known elsewhere.

Described from an unique specimen found on a laboratory table at the Hawaiian Sugar Planters' Association Experiment Station by Williams in 1930. Small colonies have been found in dry hollow twigs of papaya and pigeon pea.

Dichaetothrips setidens (Moulton).

Mesothrips setidens Moulton, 1928:129.

Cryptothrips niger Moulton and Steinweden, 1933:165, fig. 1, *d-f*.

Dichaetothrips niger (Moulton and Steinweden) Moulton, 1939:147. Synonymy by Moulton, 1944:308.

Kauai, Oahu (type locality: Manoa Valley, Honolulu).

Immigrant. I have collected this species at Oneata, Lau, Fiji; South Marutea, Tuamotu Archipelago; and Mangareva, Gambier Islands. It is also known from the Marquesas Islands.

Hostplants: *Aleurites*, *Blechnum*, *Casuarina*, guava, *Pteralyxia*, *Ricinus*.

This is our largest thrips. Some slide-mounted specimens measure 4 mm. in length. It is common in dead wood, in dried fruits, under bark and similar places and is widespread. Sakimura, in Sakimura and Krauss (1945:324-325), describes the male. Although these authors say that their collection is the second from the Hawaiian Islands, this species has long been known to some of us as a common insect of Oahu at least. See the discussion under *Diceratothrips*.

Superfamily **UROTHRIPIDEA** Hood, 1915:59

Suborder *Polystigmata* Bagnall, 1912.

This superfamily contains only one family.

Family UROTHRIPIDAE Bagnall, 1909

KEY TO THE GENERA FOUND IN HAWAII

1. Vertex of head not strongly produced . . . **Stephanothrips** Trybom.
2. Vertex of head conical, produced far distad of eyes and insertions of antennae **Conocephalothrips** Bianchi.

Genus **CONOCEPHALOTHRIPS** Bianchi, 1946:499

This monotypic genus is presumed to be endemic.

Conocephalothrips tricolor Bianchi.

Conocephalothrips tricolor Bianchi, 1946:500, pl. 28, figs. A, B, C.

Endemic. Oahu (type locality: Mount Kaala).

Hostplant: *Broussaisia arguta* (found on the leaves).

Genus **STEPHANOTHRIPS** Trybom, 1913**Stephanothrips occidentalis** Hood and Williams.

Stephanothrips occidentalis Hood and Williams, 1932:69.

Oahu.

Immigrant. Described from St. Croix and Trinidad. First recorded from the Hawaiian Islands by Moulton (1934:503) from a specimen taken at Paumalu, Oahu, by Sakimura in 1930.

Hostplant: *Paspalum orbiculare*.

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